Inter-annual and inter-colony variation in the foraging environments and behaviour of tawaki from Milford Sound

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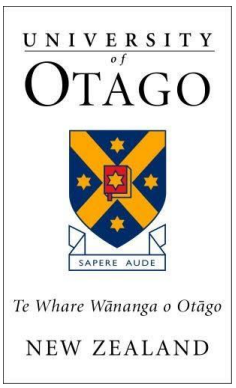

Tawaki father at Harrison Cove, Milford Sound, New Zealand, 2020.

In memory of Stephen Andrew Bowler

Whose own MSc journey was interrupted, but in the life he did lead he had already achieved so much, touched so many people's lives and lived by the example of being kind, working hard, and following your passions.

Abstract

As climate change intensifies, warming ocean temperatures, extreme weather events, and perturbations to the marine biome are becoming increasingly prevalent. A consequence of these changes are shifts in prey availability which can offset marine food webs and alter the foraging behaviours of marine predators. Seabirds are especially affected by alterations to the marine environment during the breeding season, when they are spatially constrained by the need to return to their colony and provision chicks. Thus, it is essential that their foraging habitats are productive and provide suitable conditions and prey stocks for successful foraging while minimising the energy expenditure required to locate and consume prey. To conserve seabirds in the face of significant changes to their ecosystem, it is necessary to develop a strong knowledge base of their habitat use and the degree of plasticity in their foraging behaviours.

The Fiordland crested penguin (*Eudyptes pachyrhynchus*), also known by the Maori name of tawaki, are distributed throughout New Zealand's southwestern coast and southern islands. However, little is known about the marine ecology of tawaki breeding within fiords even though fiordic systems cover a significant proportion of their range. Recent research has suggested that Milford Sound is able to buffer fiord-based tawaki from the usually detrimental effects of an El Niño year and provide them with favourable foraging conditions during their breeding season. This study presents the first comparison of guard stage foraging behaviour between two tawaki colonies from different locations within Milford Sound. Through the attachment of GPS/dive data loggers, dive parameters and spatial use were examined to determine differences in the foraging strategies of the inner-fiord colony (Harrison Cove) and the outer-fiord colony (Moraine) over the years of 2019 and 2020.

Outer-fiord birds from Moraine foraged almost exclusively outside the fiord in both years while inner-fiord birds from Harrison Cove primarily foraged within the fiord in 2020 but not in 2019. Tawaki from Harrison Cove and Moraine also displayed contrasting dive behaviour across years, either adopting a strategy of deeper, longer dives with fast velocities or shallower, shorter dives with slower velocities. Foraging efficiencies for both colonies appeared to be greater in the year 2020 than 2019 although birds foraged differently to achieve this - Harrison Cove birds dived primarily to depths of 0-20m while Moraine birds switched between shallower dives at this depth and longer dives in the deeper 60-120m of the

water column. Moraine birds adopted alternative foraging strategies across the years, with 2019 birds expending more energy on longer trips but diving shallowly while 2020 birds made shorter trips closer to their colony but exhibited higher foraging effort by diving deeply. Changes in dive behaviour across years were likely due to contrasting oceanographic factors affecting prey availability while differences between colonies reflect their differential foraging habitats.

Environmental models revealed that ocean-foraging tawaki engaged in higher foraging activity and made deeper dives with faster descent velocities over warmer water and their dive behaviour was also influenced by salinity, concentrations of chlorophyll-a and seafloor bathymetry. Although the Oceanic Niño Index proved too coarse of a measure to assess changes in foraging patterns across years, local conditions in the fiord such as the interactive effects of salinity, rainfall and wind speed, were found to impact the dive behaviour of fiord-foraging tawaki. Rainfall, salinity and wind speed are all factors that contribute to the thickness and degree of mixing in the low salinity layer (LSL). A thicker LSL, as indicated by low salinity in the upper fiord waters, increased foraging activity and caused tawaki to dive deeper, exhibiting how the lower light environment caused by a thicker LSL does not necessarily compromise the foraging of tawaki.

These findings highlight the considerable plasticity that tawaki possess in their foraging behaviours – they can forage in a range of environments and adapt their dive behaviour to fit the conditions. This bodes well for their future survival in an uncertain climate. Furthermore, this study emphasises the importance of not assuming that the foraging strategy of one colony is consistent with that of another nearby colony. Being situated in the inner fiord and within a marine reserve, has clearly influenced the foraging preferences of the Harrison Cove colony and it remains to be seen whether birds from the Moraine colony are capable of modifying their behaviour to make use of the fiord foraging habitat in years of harsh oceanic conditions and low productivity. The behaviour of tawaki across the rest of New Zealand’s fiord systems should be investigated in future to further understand the foraging opportunities fiords can provide and the significance of fiords in the conservation of this species.

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Chapter 1: General Introduction

1.1 The marine environment

Due to the dynamic nature of the marine environment, organisms that spend a part of their life history there must be well adapted to living in a highly variable system. Although, on the surface, the ocean may appear to be a relatively featureless landscape, in reality it is a vast, heterogenous environment defined by a complex system of physical and biological attributes (Hunt 1990). Physical features include the thermocline, halocline, current systems, upwelling cells, fronts, and eddies, all of which influence the abundance and distribution of marine life (Graham et al. 2001; Ainley et al. 2005). The presence and transportation of nutrients and trace elements in the ocean is largely controlled by physical processes such as currents and mixing. Light and nutrient availability determine the rate of photosynthesis, and consequently the density of phytoplankton biomass at the root of the oceanic ecosystem (Mann & Lazier 2013). Sufficient primary productivity generally supports upper trophic level animals living and foraging in the marine environment, including fish, mammals, and seabirds (Pinkerton et al. 2019).

As a result of the association between physical oceanographic attributes, primary production, and consumers, marine top predators will also strongly associate with these features and use them to locate prey (Nel et al. 2001; Bost et al. 2009). The influence and reach of different oceanographic features can exist on a fine scale (over 1-100 kilometres or hours), on a meso-scale (over 100-1000 kilometres or hours/months), or at large-scale (over thousands of kilometres or years) (Mannocci et al. 2017). Many seabird species use meso-scale physical features, including eddies, fronts, and upwelling zones (where nutrients are advected to the surface from deeper, colder waters) to locate favourable foraging patches (Cotté et al. 2007; Kappes et al. 2010). Similarly, sea surface temperature (SST) and salinity influence the foraging patterns and foraging success of seals, turtles, whales, and seabirds (Bradshaw et al. 2002; Peck et al. 2004; Etnoyer et al. 2006; Trathan et al. 2008).

Discovering how marine predators interact with and behave in their environment when searching for patchy resources is vital for managing their conservation in the future (Freitas et

al. 2008; Costa et al. 2012). At finer-scales, it is difficult to pinpoint the factors driving the foraging preferences of top predators as oceanographic features are often transient, and as a consequence, prey distributions can be highly spatially variable (Weimerskirch et al. 2005). The use of fine-scale or meso-scale environmental cues is particularly relevant during the breeding season when predators can be foraging over smaller spatial and temporal scales to provide for their young (Weimerskirch 2007; van Eeden et al. 2016; Makhado et al. 2018).

In past studies, marine organisms have shown behavioural plasticity by adapting their foraging behaviour when faced with unforeseen changes to the environment or prey dynamics (Embling et al. 2012; McIntyre et al. 2014). Of concern, the highly productive Southern Ocean has been warming more rapidly than the global ocean average (Gille 2002). Oceanic warming in the past few decades has been coupled with an increase in the strength of ocean surface winds (Meredith & Hogg 2006) which have heightened the intensity and prevalence of eddies. Plasticity in foraging habits could be vital in the future as the rise in sea temperatures occurring with climate change is likely to modify ocean productivity and subsequently alter prey distributions (Perriman et al. 2000; Hamilton et al. 2019). Furthermore, modelling projections suggest an increased likelihood of extreme events such as marine heatwaves (Oliver et al. 2018). Individuals must be able to cope with environmental variability and rapid local-level transformations to their habitat if species are to survive global changes to the marine biome (Trathan et al. 2007; Reed et al. 2009; Pichegru et al. 2010; Lescroël et al. 2014).

1.2 Foraging behaviour of seabirds

One of the key features of the life history of seabirds is that they live a dual life – breeding on land but foraging in the sea. The dissimilarity between these two contrasting habitats and the consequent constraints placed on seabirds form the basis for many of their unique shared characteristics, such as low reproductive rates, long lifespan, and delayed maturity (Ricklefs 1990; Ballance 2007). In 1968, Lack published an influential paper linking the distinct life history traits of seabirds to the availability and distribution of food in the marine environment (Lack 1968). In particular, their low reproductive rates were assumed to result from the difficulty of provisioning chicks since marine resources are patchy, scarce, and unpredictable in their distribution (Lack 1968; Ashmole 1971). However, with time and research it became

clear that this concept is lacking in nuance and there is little evidence to support the contention that prey distributions are always ‘unpredictable’ (Ricklefs 1990). Indeed, seabird life histories are related to the environmental conditions they experience, but other factors including disease, nesting sites, and predators also influence populations (Ricklefs 1990). Moreover, seabirds are capable of modifying their behaviour and exploiting spatial and temporal variation in their environment when foraging (Chimienti et al. 2017).

Breeding seabirds are known as central place foragers as they must travel regularly between foraging areas at sea and their terrestrial nest site to feed their young (Orians & Pearson 1979). As a result, seabirds must balance commuting to productive foraging zones with providing enough nutrition to their offspring or sharing incubation duties while maintaining their own body condition (Pinaud & Weimerskirch 2002; Ropert-Coudert et al. 2004a; Navarro & González-Solís 2009). Thus, there exists a range of foraging strategies that have evolved to vary the duration, distance, and output of foraging trips as related to the needs of both the chick(s) and the provisioning adult (Waugh et al. 2000; Baduini & Hyrenbach 2003).

Many pelagic seabirds will conduct short, but frequent chick-provisioning trips but if their body condition drops below a certain threshold, they can initiate a long self-provisioning foraging trip to take them to more productive feeding grounds (Weimerskirch et al. 1995; Weimerskirch 1998; Ropert-Coudert et al. 2004b). The distance from the breeding colony to productive ocean areas often determines whether seabirds will display foraging trips with this bimodal length distribution. So far, bimodal foraging trip duration has been reported most commonly in the Procellariiformes (Weimerskirch et al. 1995; Baduini & Hyrenbach 2003; Navarro & González-Solís 2009; Shoji et al. 2015) but has also been recorded in little auks (Brown et al. 2012; Jakubas et al. 2012) and multiple penguin species (Clarke 2001; Taylor et al. 2002; Saraux et al. 2011). Seabirds breeding in highly productive areas, however, are more likely to rely on local resources and to provide for their chicks more consistently using a unimodal foraging strategy (Granadeiro et al. 1998; Waugh et al. 2000).

The predictability of prey patches in both space and time can control the degree of foraging-site fidelity seabirds exhibit during the breeding season (Weimerskirch 2007; Carroll et al. 2018). For optimal foraging, seabirds will learn the location and timing of prey resources distributed in their potential foraging area and might visit the same feeding grounds successively (Hunt et al. 1999). Foraging fidelity is expected to increase in areas where

resources are predictable and associated with environmental features such as eddies, fronts, continental shelves, or other zones of high productivity (Hamer et al. 2001; Weimerskirch 2007; Kotzerka et al. 2011; Carroll et al. 2018).

Seabirds have often been advocated as useful indicators of the state of the marine environment as well as the stocks of the fish species they prey upon (Cairns 1988). Alterations in the foraging behaviour and prey preferences of seabirds have previously been associated with oceanographic factors and subsequent regime shifts in marine systems (Cury & Shannon 2004; Hatch 2013). This is particularly pertinent as seabirds have emerged as the most threatened marine taxonomic group in the world, becoming endangered at a faster pace than any other avian group (Croxall et al. 2012). It has been suggested that top predators such as seabirds could facilitate a centralised understanding of the consequences of environmental variability (Jenouvrier et al. 2003; Durant et al. 2009). Both ecosystem and climate variability over a range of temporal scales can be demonstrated through observing various seabird parameters such as diet, foraging movements, breeding productivity and population size through time (Iverson et al. 2007; Sandvik et al. 2012).

1.3 Penguin foraging ecology

All penguin species hail from the Southern Hemisphere, with most living on islands or in remote coastal regions of the southern continents. The distribution of penguins is correlated with the presence of cooler waters close to nutrient-rich cold currents that also contain a plentiful food supply (Stonehouse 1975*).* As key consumers of marine resources in the Southern Ocean, penguins play an important role in the functioning of marine ecosystems and food webs (Croxall & Lishman 1987*).* Penguins are also sensitive to changes or perturbations in these ecosystems and have become well-known as sentinels of the marine environment (Boersma 2008; Hazen et al. 2019). Being flightless, penguins are more restricted in the scope of their foraging ranges or search areas than are flighted seabirds (Dehnhard et al. 2013). Consequently, penguins must be able to locate reliable sources of food within their foraging areas in order to be successful.

The distance a penguin must travel from its nest site to reach its food supply during the breeding season varies between species and even between individuals of the same species, dependent on prey variability and breeding site location (Wilson et al. 2005; Camprasse et al. 2017a). Some penguins nest near abundant food resources, making only short foraging trips when provisioning for chicks and thus are categorised as 'inshore foragers.' Inshore foragers usually reside at their breeding sites year long. Conversely, penguins that fall into the category of 'offshore foragers' often make longer foraging trips during the breeding season (especially through courtship and incubation) (Davis & Renner 2003). When they aren't breeding, offshore foragers will make extended migratory trips to the open ocean, travelling far outside of their normal breeding ranges (Pütz et al. 2007; Mattern et al. 2018). Research on these two contrasting foraging lifestyles suggests that their origin stems from the latitude at which different penguin species breed (Croxall & Davis 1999). For example, the more southern species that occur at higher latitudes such as crested penguins (*Eudyptes*) will depart from their breeding sites to perform long migratory journeys over winter when oceanic productivity is at a low (Croxall & Davis 1999). Meanwhile, inshore foragers that breed at low latitudes such as the African (*Spheniscus demersus)* and Galapagos (*Spheniscus mendiculus*) penguin species, presumably live in an environment with a more tolerable climate and a lessened impact of seasonality on the food supply, resulting in a lack of impetus to migrate or leave the area (Croxall & Davis 1999; Saraux et al. 2011). It is also thought that the more extensive continental shelf habitat occurring at the lower latitudes of the Southern Hemisphere may further aid inshore foragers to exploit resources year-round (Croxall & Davis 1999).

The attributes of a penguin's foraging trips during the breeding season are heavily influenced by the stage of breeding; e.g. incubation vs. chick rearing (Collins et al. 1999; Barlow & Croxall 2002; Jansen et al. 2002). In the incubation stage, penguins will usually take turns sitting on their eggs with one parent foraging at a time before relieving the incubating partner (Barlow & Croxall 2002). During incubation, foraging trips are often at their longest and penguins will travel the farthest distance from their nesting sites (Lescroël & Bost 2005; Clarke et al. 2006). Once the chicks have hatched, guard stage begins where chicks are brooded by their parents. Within this chick rearing period, foraging trips are considerably shorter, often between <1-2 days long (Collins et al. 1999; Poupart et al. 2019) and parents tend to forage over shorter distances (Clarke et al. 2006). In the final stage of post-guard when both parents are out foraging and the chicks are left unaccompanied, foraging trips

increase in length and parents return to foraging over larger ranges (Moore et al. 1995; Poupart et al. 2019). These foraging trip patterns presumably occur since the food demands of the chick increase over time (Culik 1994) so parental foraging trip durations must increase, with both parents provisioning in order to match the chicks' growing nutritional requirements (Clarke et al. 2006).

Whereas early research on penguin biology was primarily land-based, the advent of tracking technology and data-logging devices has provided researchers with new insights into the relationship between penguin foraging patterns and oceanographic processes (Wilson et al. 2002; Wilson 2004). Oceanic fronts are systems where water masses of distinct properties meet and create zones of nutrient upwelling with increased productivity (Ainley & Jacobs 1981; Schneider 1990). Multiple penguin species, including royal penguins (*Eudyptes schlegeli*) and king penguins (*Aptenodytes patagonicus*), have exhibited a use of fronts (Bost et al. 1997; Hull et al. 1997) when foraging. The Subantarctic front is often targeted by macaroni penguins (*Eudyptes chrysolophus*), which also focus their foraging activity around dynamic areas comprising eddy fields and filaments formed by turbulent stirring (Bon et al. 2015). Highly productive upwelling zones where deep water and nutrients are brought to the surface, are an oceanographic feature associated with the occurrence of all four penguin species in the *Spheniscus* genus (Boersma 1978; Culik & Luna-Jorquera 1997; Boersma et al. 2007; Crawford et al. 2007).

Scientists are only just beginning to understand the variety of physical structures and variables in the marine environment that influence or guide penguins during their foraging journeys. Both Adelie (*Pygoscelis adeliae*) and Magellanic (*Spheniscus magellanicus*) penguins respond to tidal switching regimes by altering their foraging locations and moving to foraging areas via tidal currents (Rey et al. 2010; Oliver et al. 2013). By making use of tidal systems, penguins reduce their energy expenditure while following the ebbs and flows of changing prey availability. King penguins also tend to swim with the current on their foraging trips (Baylis et al. 2015) and preferentially forage in mesoscale frontal zones defined by sea surface temperature gradients (Cotté et al. 2007). Crested penguin species such as the rockhopper (*Eudyptes chrysocome)* and macaroni have reportedly used temperature, currents, fronts and eddies as cues to locate optimum foraging conditions in the open ocean (Bon et al. 2015; Whitehead et al. 2016).

The impact of climate change on the marine environment is an emerging threat to penguin populations. Rising ocean temperatures and an increase in ocean acidity will likely lead to the seas of the Southern Ocean experiencing trophic shifts and decreased primary productivity (Ramírez et al. 2017). This will reduce the food supply for marine predators such as penguins. Furthermore, a projected increase in the occurrence and intensity of sea surface temperature anomalies might also cause a misalignment between the peak breeding period in penguins and marine productivity (Ramírez et al. 2017). The reliability of oceanographic features in guiding penguins to prey could therefore be diminished, reducing the foraging success of penguins and decreasing their capacity to provide for their chicks, thus lessening reproductive success. Multiple studies have already implicated rising sea surface temperatures as key drivers behind population declines in penguin populations (Taylor 2000; Hilton et al. 2006; Le Bohec et al. 2008; Morrison et al. 2015; Mattern et al. 2017). Obtaining valid baseline data and knowledge of a species' foraging habits and resilience to environmental change is vital in order to develop the most informed plan for their future protection. This is particularly true for penguins, considering how their population numbers vary with the availability of prey (Weimerskirch et al. 2003; Mattern et al. 2009), thus an understanding of their foraging ecology is necessary to assess their current status and deliver conservation actions as appropriate.

1.3.1 New Zealand penguins

There are six distinct penguin species which breed in the New Zealand region with three of these species (eastern rockhopper penguin *Eudyptes filholi,* snares crested penguin *Eudyptes robustus* and erect-crested penguin *Eudyptes sclateri*) breeding on New Zealand's Subantarctic Islands. The remaining three species (little penguin *Eudyptula minor,* yellow-eyed penguin *Megadyptes antipodes* and Fiordland crested penguin *Eudyptes pachyrhynchus*) breed on the New Zealand mainland. The little penguin and yellow-eyed penguin are classified as inshore foragers, while the other four species are offshore foragers (Davis & Renner 2003). The oceanographic regions surrounding the breeding habitat of most New Zealand penguins are marked by important marine features, such as the Subtropical Front and Subantarctic Front (Heath 1981). These features have considerable influence over the movements and foraging ecology of penguins at sea (Mattern 2007). Even with the current

research, we are only beginning to scratch the surface of investigating the foraging ecology of New Zealand penguins, especially in regard to determining the marine processes and environmental factors driving their at-sea behaviour.

Although New Zealand is widely considered a penguin hotspot (hosting a third of the world's penguin species, four of which are endemic), comparatively little is known about New Zealand penguins compared with other penguin species around the world (Mattern & Wilson 2019). This is particularly concerning, given that five of our six species are near threatened or in decline and the key causes of these declines remain mostly unknown (Mattern & Wilson 2019). More research is necessary to pinpoint the real threats to New Zealand's penguins and to prepare us to conserve these species in the face of heightened pressure from anthropogenic sources such as climate change, tourism expansion, pollution and fisheries bycatch. Unlocking the marine sentinel potential in New Zealand's penguins through further research will allow scientists to demonstrate the impact of climate change in a critical area of the Southern Ocean.

1.4 Tawaki

The Fiordland crested penguin, also known by the Māori name of tawaki, were once known as the third rarest penguin species in the world (Mattern 2013). Tawaki are endemic to New Zealand and breed in the temperate rainforests of the south-west coast of the South Island and Stewart Island (Davis & Renner 2003). Under the IUCN Red List, tawaki are listed as 'Near Threatened' with a decreasing population trend due to their perceived decline in recent decades (Birdlife International 2021). The current population is thought to stand at around 12,500-50,000 mature individuals (Birdlife International 2021) with this wide range indicating the high uncertainty in population numbers as many potential breeding habitats for tawaki within Fiordland are yet to be surveyed. In the past, numbers of tawaki were often underestimated. For example, a ground survey conducted in Milford Sound in 2016 located 77 nests, leading to an estimate of 130-150 breeding pairs in one fiord (Mattern & Long 2017), in contrast with the nine nests reported there in the 1990s (McLean & Russ 1991). Tawaki have been cited as the fifth least studied penguin (Mattern & Wilson 2018) and before the inception of The Tawaki Project in 2014 (https://www.tawaki-project.org/), little

was known about their marine ecology. Headed by penguin researchers Thomas Mattern and Ursula Ellenberg, The Tawaki Project marks the first major attempt to elucidate key facets of tawaki ecology since the 1980s (Mattern & Ellenberg 2014).

1.4.1 Threats to tawaki

Although tawaki appear to be faring better than some New Zealand penguin species (Mattern & Wilson 2018), they still face threats from terrestrial predators across South Westland and Fiordland. During the breeding season, stoats (*Mustela erminea*) are the main introduced predator that is capable of causing large-scale tawaki chick mortality and impacting colony reproductive success. At Jackson Head in 2016, chick disappearances ceased only after three stoats were removed by trapping (Mattern & Wilson 2018). Although Taylor (2000) implicated rats (*Rattus spp.*), and brushtail possums (*Trichosurus vulpecula*) as further possible predators of tawaki eggs/chicks, there is little evidence to support this claim. These predators co-occur with tawaki at multiple sites and although they will occasionally investigate nests, chick predation or harassment of adult penguins has not been observed (Wilson & Long 2018). Native weka (*Gallirallus australis*), however, are known predators of tawaki eggs and chicks (McLean 1990; St Clair 1992). It appears though, that the impact of weka on tawaki populations hasn't been severe enough to cause major declines as both tawaki and weka remain common on islands where weka have been recently introduced (Taylor 2000).

While introduced predators, human disturbance (Ellenberg et al. 2015), and fisheries-related mortalities (Crawford et al. 2017) are all threats the species is currently facing, a serious and rather unmanageable threat to tawaki populations is the capacity for earthquakes and environmental disasters in the South Westland and Fiordland regions (Mattern & Wilson 2018). Throughout the breeding range of tawaki there has been a considerable amount of seismic activity and more is forecasted in the future. It is projected that within the next few decades an earthquake of at least magnitude 8 will occur in South Westland (Biasi et al. 2015). The resulting landslides, ground ruptures, and avalanches from such a high magnitude earthquake would cause severe damage to coastal tawaki breeding habitats. The impact on the population would be particularly dismal if it occurred when the penguins are on land at their colonies during part of the breeding season (June-September) or the moult (mid-January-

February). There have been similar instances in the past where landslides and extreme environmental events have impacted other penguin species (Cuthbert et al. 2009; Chilvers & Hiscock 2019).

Aside from the future potential for environmental disasters, the most unpredictable and far-reaching danger to tawaki might be the increased frequency of marine perturbations associated with climate change. Rising sea temperatures can alter marine productivity and affect the abundance or distribution of prey (Perriman et al. 2000; Browne et al. 2011). Warming ocean temperatures have been linked to population declines and the reduced survival of adults and fledglings in New Zealand penguin species such as the yelllow-eyed penguin (Mattern et al. 2017) and eastern rockhopper (Morrison et al. 2015). Further evidence also indicates how climate change is positively associated with an increase in the severity and frequency of extreme weather events such as the El Niño-Southern Oscillation (ENSO) (Vargas et al. 2007; Cai et al. 2014; Cai et al. 2015). In 2015, an El Niño, unprecedented in strength, led to sub-optimal ocean foraging conditions for tawaki at Jackson Head on the West Coast and resulted in an abysmal breeding season (Mattern & Ellenberg 2015). However, in this same year, tawaki breeding at the Harrison Cove colony in Piopiotahi/Milford Sound had an exceptional breeding season with several pairs even raising two chicks to fledgling stage (Mattern & Ellenberg 2015). This was a particularly notable discovery given that tawaki were previously thought to be brood reducers, able to raise only one chick from the two eggs laid (St Clair 1992). Furthermore, the Harrison Cove birds mainly foraged within the fiord, on average remaining within a 2km radius of their colony – a drastically different foraging strategy from that of the Jackson Head birds which swam up to 100km offshore in an attempt to provide for their chicks (Mattern & Ellenberg 2015).

Although the underlying mechanics are unknown, the fiord system seemed to buffer fiord-breeding tawaki from the unfavourable foraging conditions in the open ocean during an extreme weather event. The foraging habits of fiord-breeding tawaki require further investigation to determine the value of this habitat and whether fiords can act as strongholds for the species in future climatic or oceanic disturbances.

1.4.2 The breeding cycle of tawaki

After spending three months at sea, foraging within the Subantarctic waters below New Zealand and Australia, tawaki begin returning to their breeding colonies from mid-June and July. Tawaki colonies usually consist of loose aggregations of nests located several metres apart, although sometimes, particularly when under boulders or in sea caves, multiple pairs might nest within one to two metres of each other (Davis & Renner 2003). Tawaki often nest in cryptic or inaccessible places within tree roots, sea caves, or under boulders and many pairs tend to return to the sites they used in previous years (Warham 1974).

Two dimorphic eggs are usually laid 3-6 days apart in late July to early August and while egg laying is mostly synchronised within colonies, it can vary between sites by up to 2-3 weeks (Ellenberg et al. 2015). Incubation commences after the laying of the first egg and after 5-10 days of shared incubation, the female will make the first foraging trip of almost two weeks before the male then spends a similar period of time away (Warham 1974; St Clair 1992). In total the incubation period lasts about 32 days before the second egg hatches with the male returning a few days prior (Warham 1974; St Clair 1992; Figure 1.1). The smaller chick from the first-laid egg will likely die from starvation within the first few days although it has been noted that in years where the food supply is abundant, some tawaki pairs are able to fledge both chicks (Warham 1974; McLean et al. 2000; Mattern & Ellenberg 2016). During post-guard, the male will guard the chick while the female typically makes daily provisioning trips until chicks begin to creche at 2-3 weeks of age (Figure 1.1). Both parents will then make longer foraging trips to feed the growing chick (although the female will provide the bulk of the food), until it fledges at around 75 days in mid-November to early December (Warham 1974; Figure 1.1).

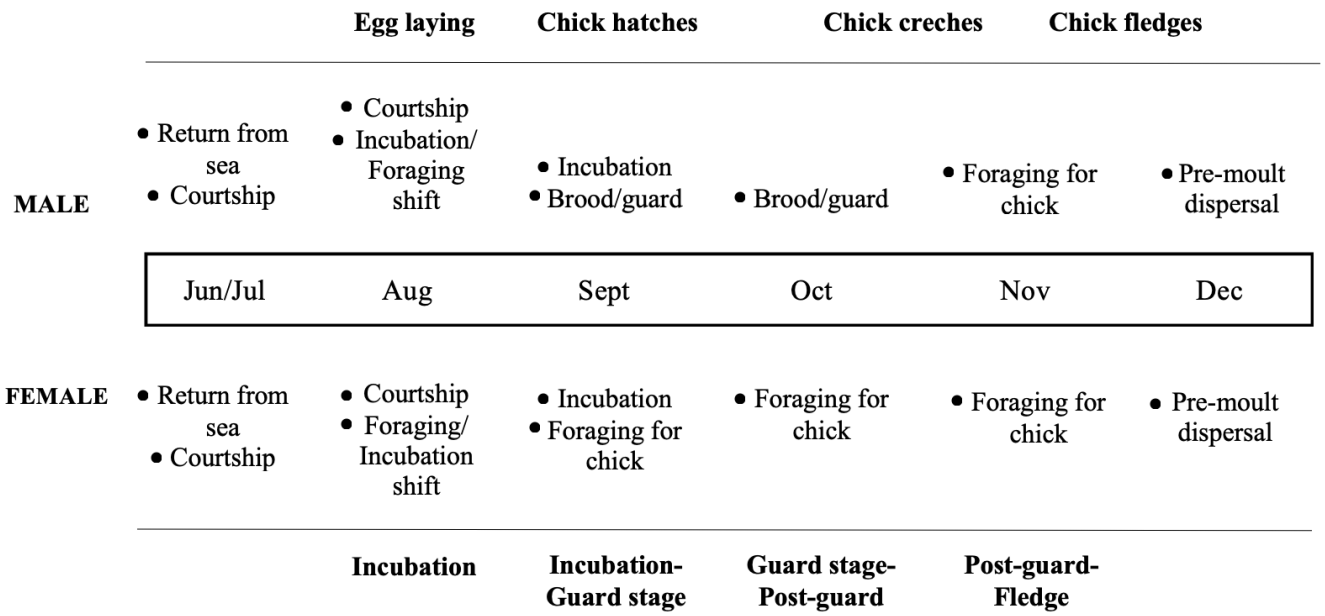

Figure 1.1 General overview of the breeding cycle of tawaki and the respective roles of male/female parents.

1.4.3 Tawaki diet & foraging habits

Early studies reported a tawaki diet consisting of cephalopods, crustaceans and fish (van Heezik 1989, 1990) and this has been corroborated by more recent work detailing δ15N values from blood samples that align well with a squid-dominated diet (Flemming & van Heezik 2014; Poupart et al. 2019). There appears to be no clear sex differences in prey preference as well as generally low prey diversity (van Heezik 1989; Poupart et al. 2019). It is important to note, though, that the study by Poupart et al. (2019) was carried out over a fraction of the species' total range and tawaki populations elsewhere could experience contrasting marine conditions. For example, the diet of tawaki on Whenua Hou/Codfish Island was fish rather than squid-dominated, although diet sampling was only carried out over a short period of time (van Heezik 1990). The uniqueness of the ecosystem within which fiord-living tawaki forage may also lead to a reliance on different types of prey. However, an isotopic study comparing the diet of tawaki at Milford Sound with that of tawaki at a coastal site (Jackson Head) and Whenua Hou detected no significant differences in stable isotope

values from blood and feather samples (White 2020). More recent dietary analyses used DNA sampling from the faecal matter of birds at Jackson Head and found fish were the most common prey of tawaki, occurring in 75% of samples, followed by cephalopods and krill (Mattern et al. in press). Given the results of past studies, tawaki generally seem to maintain a diet of small fish or fish larvae and cephalopods.

While a few dietary studies have been conducted, less is known of the foraging behaviour and environmental variables impacting the foraging patterns of tawaki (Mattern 2013). Individuals tracked at Open Bay Island off the coast of South Westland (Figure 1.2) were found to extensively use habitat on the continental shelf-slope within 42km of the colony (Poupart et al. 2019). The duration of foraging trips during guard stage were 8−41 h (11−134 km) while the longer 2-7 d (42- 115 km) foraging trips occurred, as with other penguin species, during the incubation and creche stages (Poupart et al. 2019). Dives took place primarily in the epipelagic zone during daylight (Poupart et al. 2019).

Results from the last five years of data collection by The Tawaki Project at three different sites (Figure 1.2) also suggest pelagic foraging. Guard stage foraging at Jackson Head usually occurred 30-60km out from the colony or even up to 80km during particularly bad conditions such as those of the El Niño of 2015 (Mattern & Ellenberg 2015, 2018). The maximum dive depth was 96m in one individual although the majority of dives did not occur beyond 40m (Mattern & Ellenberg 2018). At Whenua Hou, foraging ranges varied substantially with some birds remaining inshore within 5km of the breeding colony while others would forage 10-30km north-west and west of the island (Mattern & Ellenberg 2018, 2017). Those that foraged inshore stayed in the top 20m of the water column while those foraging further offshore dived between 30-50m deep – closer to the sea floor. At Milford Sound, most inner-fiord birds used small foraging ranges within the fiord and usually dived to depths that would seldom exceed 30m while venturing an average of 4km out from the colony (Mattern & Ellenberg 2018, 2017). Many birds even stayed within Harrison Cove itself although the occasional bird did make a foraging trip outside the fiord. These findings seem to suggest that tawaki have considerable plasticity in their foraging with different colonies exhibiting distinctive behaviours across a range of contrasting environments.

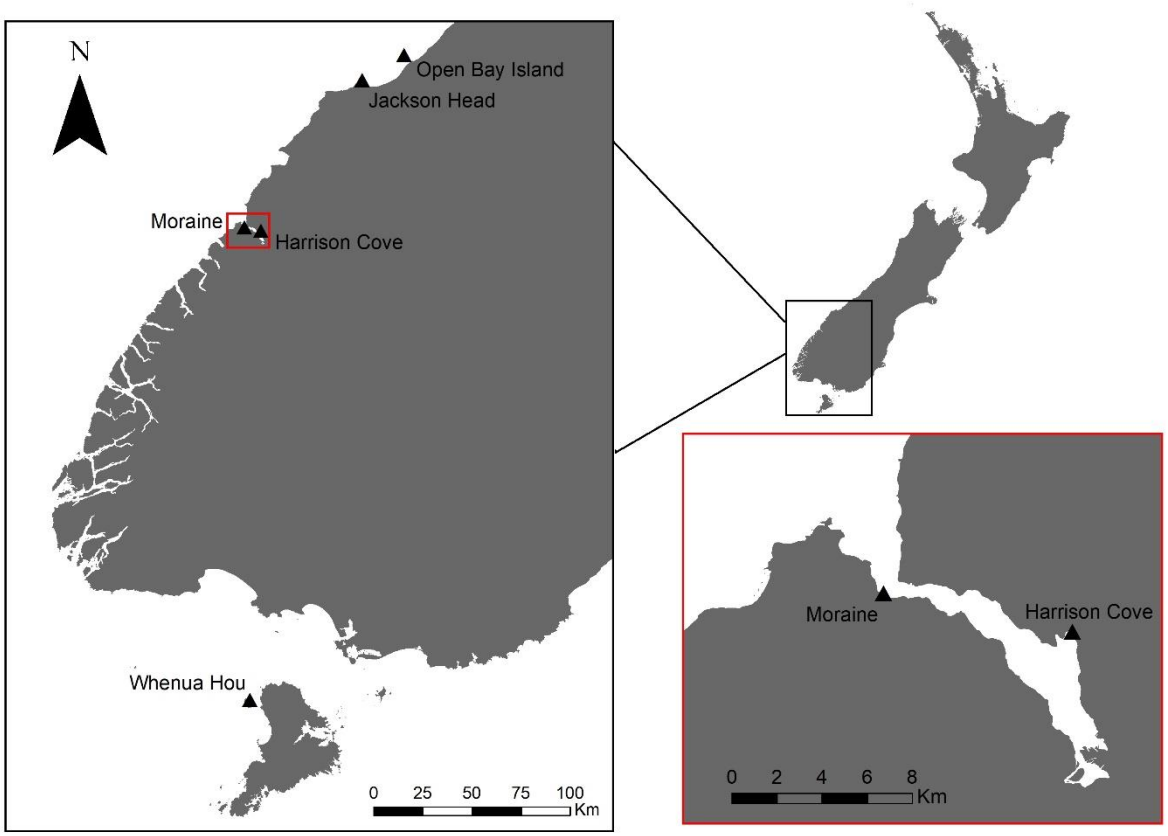

Figure 1.2 Map of tawaki colonies that have been studied in the past (Open Bay Island, Jackson Head, Harrison Cove and Whenua Hou) and are part of the current study (Harrison Cove and Moraine). Red inset map shows a close up of Milford Sound, with the outer-fiord colony of Moraine and inner-fiord colony of Harrison Cove.

1.5 The fiord setting

Milford Sound is a fiord of 15km in length, located on the southwest of New Zealand's South Island. It hosts multiple colonies of tawaki with an estimated total population of 130-150 breeding pairs (Mattern & Long 2017). The Moraine colony is by far the largest, hosting approximately 50 nests, followed by Harrison Cove with around 20 nests, while 10 nests can usually be found at the two smaller colonies of Anita Bay (outer-fiord) and Sinbad Gully (inner-fiord) (Mattern & Long 2017). Two other significantly smaller and harder to access breeding sites exist at Penguin Cove and Cascade Beach (see map in Mattern & Long 2017). Tawaki also breed in a number of other fiords across Fiordland, such as Doubtful Sound, Thompson Sound, Break Sea Sound and Dusky Sound, although their population numbers

within these areas are yet to be determined. A variety of environmental attributes within fiords such as wind shear or the thickness of the low salinity layer (LSL), likely aid in determining the foraging routes of tawaki and whether they will staywithin fiord to forage or venture outside to the coastal ocean.

There remains a gap in our knowledge on how and why fiords may provide tawaki with suitable foraging conditions and be sheltered from the effects of marine perturbations such as El Niño. These habitats could be vital for the future survival of the species, which faces an increased frequency of environmental disturbance from extreme weather events. The significance of fiord ecosystems in the species' foraging strategies can be investigated by comparing the foraging behaviour of breeding tawaki at the entrance of fiords to that of tawaki breeding at colonies deeper within the fiord. Outer-fiord tawaki situated at the fiord entrance might benefit from more foraging options provided they are sufficiently flexible in their foraging behaviour, as they have both easy access to the open ocean as well as the fiord, where they could evade poor oceanic conditions during environmental disturbances. By contrast, if an outer-fiord colony solely uses the open ocean while an inner-fiord colony uses the fiord, this could indicate how colony location results in the spatial separation of foraging environments, which could lead to reproductive consequences in years when marine conditions are unfavourable.

1.6 Research aims

My overarching aim is to investigate the foraging ecology of two colonies of tawaki breeding in a fiord ecosystem and assess the significance of environmental variables in determining their dive behaviour.

To achieve this, my investigation can be split into two objectives:

1. To compare the foraging movements and dive behaviour between outer-fiord (Moraine) and inner-fiord (Harrison Cove) tawaki breeding colonies at Piopiotahi/Milford Sound across two consecutive breeding seasons (2019 and 2020).
2. To align tawaki foraging data with environmental factors in the fiord or ocean environments that might influence the foraging behaviour of tawaki, using data derived from satellites (e.g. temperature, chlorophyll-a-a), local weather stations (i.e.

National Climate Database) and direct measurements (e.g. salinity and temperature in the fiord).

1.7 Thesis structure

To achieve my research objectives, data on the spatial use and dive behaviour of tawaki were collected using dive and GPS logging devices. Fine-scale environmental data were compiled in order to identify the main factors influencing the dive behaviour of tawaki foraging in different environments. This thesis is structured with the central chapters (chapters two and three) written as stand-alone papers, and as a result, the chapters contain a degree of repetition, mainly in the introduction and methods sections. Cross referencing between chapters is used occasionally to minimise repetition.

The overall thesis structure is outlined below:

Chapter 1 outlines the background rationale and the main aims of the study.

Chapter 2 describes differences in spatial foraging parameters and dive behaviour of tawaki breeding from two different colonies, over two consecutive breeding seasons in Milford Sound.

Chapter 3 investigates the influence of environmental factors on the dive behaviour of fiord-foraging and ocean-foraging tawaki.

Chapter 4 synthesises the key findings and presents the conclusions and implications of this project.

Chapter 2: The inter-annual and inter-colony foraging and dive behaviour of tawaki from Milford Sound

2.1 Introduction

During the breeding season, penguins become central place foragers as their need to frequent land-based nesting sites to provide for their chicks can force a reduction in their foraging ranges (Williams 1992; Trathan et al. 1998; Hul11997). Previous work has suggested that individuals rely on prey that are readily available close to their colony sites (Hennicke & Culik 2005; McCutcheon et al. 2011). Although penguins may extend their foraging ranges considerably during incubation and post-guard, parents from a range of penguin species tend to make daily trips and keep tighter foraging ranges during guard stage when the chick is most vulnerable and in need of regular feeding (Collins et al. 1999; Poupart et al. 2019). When range is restricted, adjusting dive performance can be critical to enhancing a bird's foraging success in areas of low prey availability or in response to environmental changes (Lescroël & Bost 2005; Berlincourt & Arnould 2015).

Multiple factors have been found to influence the foraging behaviour of penguins. For example, physical features of the marine environment, such as salinity, sea surface temperature, bathymetry and oceanographic features may alter dive patterns (Lescroël & Bost 2005; Ramírez et al. 2014; Sutton et al. 2020). Other studies have reported foraging behaviour to vary according to individual characteristics such as age (Le Vaillant et al. 2013) and sex (Bethge et al. 1997; Pichegru et al. 2013). Further variables include the abundance of prey and the species of prey being pursued (Hennicke & Culik 2005; Miller & Trivelpiece 2008). Temporal variables such as the year and season have also been reported to impact dive behaviour although this may be a result of their correlation with the distribution of prey species (Watanuki et al. 1993; Camprasse et al. 2017a). The marine environment can vary considerably from year to year, especially in response to marine perturbations such as La Niña/El Niño. Natural marine climate phenomena are not the only events that may impact predator-prey dynamics and the physical attributes that modulate foraging though; anthropogenic impacts are also increasingly affecting the behaviour of marine life (Preston et al. 2008; Chilvers et al. 2014).

Contrasting environmental conditions, abiotic factors, and prey availability can all come into play when a seabird species has colonies in markedly different locations (Chiaradia et al. 2007; Hoskins et al. 2008; Gulka et al. 2020). A study of rockhopper penguins at three different sites with varying ecological conditions demonstrated the impact that distinct environments can have on daily foraging trip characteristics (Tremblay & Cherel 2003). Often, colonies can be located relatively close to each other and yet foraging behaviour of individuals from each colony will still diverge significantly (Chiaradia et al. 2012). Some researchers theorise that when central-place foraging occurs during the breeding season, this leads to strong intra-specific competition which subsequently results in between-colony spatial segregation and differences in foraging behaviour (Sánchez et al. 2018; Bolton et al. 2019; Ito et al. 2021). One study of little penguins revealed that even individuals from colonies with overlapping foraging ranges had significant differences in their trophic position, prey size and diet composition (Chiaradia et al. 2012). It is also possible that individuals from different colonies show plasticity in their dive behaviours and yet still exert similar levels of foraging effort within a season (Hoskins et al. 2008). Whether or not individuals from a colony are disadvantaged by their site locality and foraging behaviours will directly impact their reproductive output and fledging success (Chiaradia et al. 2007).

Using successful foraging strategies is vital during the chick rearing period since failure to acquire sufficient prey can impact offspring growth and quickly result in chick death (Davoren & Montevecchi 2003; Lescroël et al. 2010). Diving behaviour is often a reflection of the type of prey being pursued and/or the foraging habitat and consequently, diet and site fidelity decide the consistency of dive behaviour (Elliot et al. 2008; Woo et al. 2008). Past studies on the foraging behaviour of penguins have exhibited how different species can exhibit varying levels of individual consistency dependent on their foraging strategies, for example, the generalist gentoo penguins (*Pygoscelis papua*) display high individual consistency in foraging behaviour while little individual consistency is shown in the intermediate generalist Adelie penguins (Herman et al. 2017). In ecology, the measure of 'repeatability' is widely used to determine the degree of inter-individual and intra-individual consistency (Wolak et al. 2012). Repeatability testing is just beginning to be used by penguin researchers to investigate inter-individual consistency in foraging and diving parameters (Traisnel & Pichergru 2019; Michelot et al. 2021). Repeatability has the potential to be a metric of considerable interest as it can indicate the degree of behavioural plasticity present in

individuals of a species and thereby demonstrate their capacity to adapt to environmental change.

While the diving behaviour of New Zealand species such as yellow-eyed penguins and little penguins has been studied in detail, only one article has been published that highlights the foraging behaviour and dive habits of tawaki during the breeding season. This study by Poupart et al. (2017) reported individuals from Taumaka/Open Bay Island made foraging trips of a shorter distance during guard stage and dived predominantly within the epi-pelagic zone. Open Bay Island is situated off the coast of South Westland, over 100km away from Milford Sound (see Chapter 1, Figure 1.2). It is likely that birds from Open Bay Island are navigating environmental conditions very different to those that Milford Sound tawaki experience, especially since tawaki in Milford Sound nest in a fiord rather than on an island or on the coastal mainland. When foraging within New Zealand fiords, birds will be exposed to lower degrees of salinity due to freshwater inputs, decreased light penetration at deeper depths, unique bathymetry, and a lack of the usual open sea oceanographic variables (Miller et al. 2006). There are also no studies that compare the diving and foraging behaviours between two colonies of penguins that inhabit different locations within the same fiord.

The Tawaki Project has previously studied tawaki foraging in Milford Sound and compared their foraging behaviours to tawaki foraging at a coastal site in South Westland (Jackson Head) and on Whenua Hou (Mattern & Ellenberg 2015, 2016, 2017, 2018; see Chapter 1, Figure 1.2). Milford Sound tawaki from the Harrison Cove colony had substantially different dive and foraging behaviours compared to the other sites, with tawaki often foraging shallowly and within the confines of the fiord – usually within 4km from their breeding site. In contrast, tawaki from Whenua Hou and Jackson Head often travelled further and used more of the water column when diving, displaying different foraging strategies relevant to their distinct foraging environments. The current study aims specifically to focus on tawaki breeding in Milford Sound to determine whether the shallow-diving behaviours and fiord-foraging habits of the Harrison Cove colony in the past are shared across other colonies breeding in the fiord. To test this, the study will compare the inner-fiord colony of Harrison Cove with a colony situated in the outer fiord, near the opening of Milford Sound over a two-year period.

Tawaki from different areas clearly demonstrate flexibility in foraging strategies and based on findings from studies investigating foraging differences between penguin colonies, there

will likely be differences in foraging and diving behaviour between the Moraine and Harrison Cove colonies in Milford Sound. I made the following predictions:

1. Birds from the outer-fiord colony of Moraine will primarily forage in the ocean as it is the natural foraging environment of most coastal tawaki colonies, whereas birds from the inner-fiord colony of Harrison Cove will primarily forage in the fiord, as it is the foraging environment immediately accessible to them and they have foraged solely within the fiord in past years.
2. The foraging trip parameters such as trip duration, maximum distance from the colony and total distance travelled will be greater for Moraine birds than Harrison Cove birds, reflecting the increased foraging effort of ocean-foraging birds compared to birds that forage in the nearby fiord.
3. The foraging and diving behaviour of Moraine and Harrison Cove birds will alter with time – both over the hours of the day and between the years 2019 and 2020, likely as a result of differing environmental conditions within the fiord and in the surrounding marine environment.
4. Moraine birds foraging in the open ocean outside of the fiord, will make longer and deeper dives more often than fiord-foraging Harrison Cove birds that may be diving for different prey items at shallower depths due to the lower light environment in the fiord compared to the ocean.
5. Between individuals in the population and between individual's multiple foraging trips, tawaki will show low repeatability in their dive behaviour as past work has demonstrated how individuals show considerable flexibility and are able to use a range of different diving strategies, dependent on the foraging environment.

This study presents the first comparison of foraging behaviour between tawaki colonies at two different locations within the same fiord. Through the use of data loggers that acquire GPS fixes while recording the depth and time of dive events, a number of foraging and dive parameters were examined to determine behavioural differences between colonies over the years of 2019 and 2020. To minimise confounding factors and other potential sources of variation in dive behaviour, tawaki were tracked only during the chick-guard breeding stage. As a result, this also eliminated any influence of sex on dive behaviour as female tawaki are the sole providers for their chicks during guard stage while the male is left to brood the chick. Therefore, with only guard-stage females being tracked across colonies and across the years

of 2019 and 2020, differences in dive behaviour are likely a result of individual/colony-based behavioural plasticity in response to the different physical environments in which birds forage. Furthermore, the diving and foraging preferences of tawaki may change depending on the unique environmental and biological conditions they are faced with across years.

2.2 Methods

2.2.1 Study area

This study was conducted at Milford Sound, Fiordland (44.6414° S, 167.8974° E), a fiord on the southwest of New Zealand's South Island. This fiord hosts multiple colonies of tawaki with an estimated total population of 130-150 breeding pairs (Mattern & Long 2017). The fiord is located within Fiordland National Park and 690 hectares of the northern side of Milford Sound is protected by the Piopiotahi Marine Reserve. As one of New Zealand's most popular tourist destinations, Milford Sound receives a considerable amount of boat traffic from nature cruise tour operators.

Individuals were sampled from two sites - Harrison Cove, an inner-fiord colony site and Moraine, an outer-fiord colony site. The Harrison Cove colony (-44.624°, 167.913°) lies near the mouth of the Harrison River while the Moraine colony (-44.604°, 167.809°) is situated on the southern side of the fiord, near the fiord entrance and opposite Dale Point. . Harrison Cove hosts a breeding colony of roughly 16-20 breeding pairs while the Moraine Colony is much larger, hosting around 50 breeding pairs, 25 of which were found in the section of the colony I sampled. An average night during post-guard in Harrison Cove usually sees about 15-20 birds returning at the main landing site whereas one night at Moraine sees 75-95 birds landing. The vegetation and landscape of Harrison Cove and Moraine also differ. Harrison Cove hosts some fern-and fuchsia (Fuchsia excorticata) dominated areas and is less rocky than Moraine which has vegetation typical of coastal Westland such as kiekie (Freycinetia banksii) as well as large rata (Metrosideros umbellata). Moraine also hosts more complex underground rock systems for tawaki to nest in than at Harrison Cove (see Mattern & Long 2017).

2.2.2 Deployment and retrieval of data loggers

Research took place over two consecutive breeding seasons in 2019 and 2020. GPS dive loggers were deployed on adult females when penguin pairs were in the chick guard stage of

breeding. Due to issues with the permit process, the 2019 field season began late, on the 27th of September and continued until the 19th of October. As a result, the sample size for the 2019 Harrison Cove colony was smaller than anticipated as many of the birds were already in post-guard. In 2020, fieldwork began on the 8th of September and continued through to the 15th of October. The 2020 field season saw some exceptionally bad weather with storms and high winds sweeping over Milford Sound every week. This made it more difficult to reach the outer-fiord colony, Moraine, as it is closer to the open sea and therefore quite exposed, unlike the sheltered environment of Harrison Cove. Consequently, my 2020 sample size for the Moraine colony was smaller than my sample from Harrison Cove, since logistically I was only able to make one round of deployments at Moraine before the weather prevented access. When I was able to reach the site again for device recovery, almost all the birds were in post-guard and forecasts of future storms forced me to suspend any further deployments.

On their return from foraging, and after allowing them time to feed their chicks and rest, adult females were captured at the nest by hand, or with the aid of a leg crook for the more inaccessible nests. Once captured, birds were fitted with a cloth hood to minimise stress and weighed using a 5kg spring scale (±10g; Pesola). To quantify their foraging movements, habitat use, and diving behaviour, birds were equipped with a combination GPS dive logger (Axy-Trek Marine, Technosmart) recording location, depth (±10 mbar of pressure), and temperature (± 0.2°C) every 1 s and tri-axial body acceleration at 25 Hz (40 x 20 x 8 mm, 14g). In 2019, the loggers were programmed to take 1 fix per minute, excepting throughout the non-peak foraging period of 2300-0400 h (when tawaki are either on land or asleep floating on the water surface), they were programmed to take 1 fix every 15 minutes. In 2020, a different programming regime was used to attempt to extend the devices' battery life and to gain data on multiple foraging trips. The 2020 loggers' sampling regime was thus set to record a GPS position every 3 minutes or every second dive (an average tawaki dive lasts 1.5 minutes). Similar to the 2019 regime, between the non-peak foraging period of 2300-0600 h, the devices were programmed to take a fix only every 15 minutes.

Since acquisition of a GPS fix takes between 25 and 30 seconds, no position could be recorded when a penguin stayed at the surface for shorter intervals between dives. Unfortunately, tawaki often spent very short periods of time at the surface after diving, so GPS data were often quite patchy. In addition, it is much harder for the devices to take a successful GPS fix when tawaki forage exclusively within the fiord, as the environment is

closed in by mountains that can block access to satellites. Thus, tawaki that foraged in the open sea often had more detailed and cohesive GPS tracks than tawaki that foraged solely in the fiord.

The devices were attached to the midline dorsal feathers on the lower back with waterproof tape (TESA 4651; Beiersdorf AG) following Wilson et al. (1997). In total, attached devices represent well under 1% of the penguins' body mass in air and are therefore likely to have negligible impact on the individual's foraging behaviour (Agnew et al. 2013). Tawaki weigh an average of 3.7 kg, with a weight range of 2 to 5.95 kg and the 14g GPS loggers thus only contribute to 0.007% of the body weight of the lightest possible tawaki (at 2kg, 14g/2000g = 0.007). Handling procedures lasted ~10 minutes before birds were released near their nest to resume normal behaviours. Trail cameras were deployed at the nests of logger birds in order to monitor nest attendance patterns and aid with planning their recapture. After 4-5 days of wearing the device (their projected maximum battery life), individuals were recaptured, and the data loggers removed. Devices were recovered by either recapturing logger-equipped penguins shortly after their landing on an access track to their colony site or by recapturing them at the nest if they were initially missed at the landing.

In 2016, The Tawaki Project used trail cameras to monitor nest attendance patterns of birds fitted with GPS dive loggers and compare them with those of control groups at three different sites and reported no measurable effect of the GPS devices on behaviour (Mattern & Ellenberg 2017). Foraging trip lengths were found to be comparable between penguins in the experimental and control groups (Mattern & Ellenberg 2017). Furthermore, ship-based observations of logger birds in Milford Sound also indicated that their diving duration and frequency was similar to that of penguins not carrying external devices. I therefore conclude that the behaviour of tawaki is not significantly impacted by carrying a device and the dive data collected can be reliably interpreted.

2.2.3 Data analysis

Comparison of foraging parameters and ranges between years and colonies

Foraging Parameters

Foraging parameters of maximum distance from the colony per trip, cumulative distance travelled per trip and horizontal travelling speed were calculated from GPS location data

using a custom-written script in Matlab 9.9 (Mathworks, Inc., Natick, MA, USA). The foraging metric of trip duration was also calculated per bird per trip over the two colonies and years. One of the birds tracked in Harrison Cove in 2019 had a data logger that was not correctly programmed, and thus could not be included in the foraging or dive data analysis but could be included when analysing the parameter of trip duration. For the foraging parameter analysis, the trips of each bird were averaged to obtain a value for each individual prior to analysis. As a result of having non-normal distributions, transformations were applied for analyses of three of the four foraging parameters, a log 10 transformation was used for the trip duration and maximum distance from colony per trip, while a natural log transformation was used for distance travelled. The horizontal travelling speed did not require transformation for analysis. Using R, an ANOVA was performed on the foraging parameters (averaged per bird) to test the effects of year (2019/2020) and colony (Moraine/Harrison Cove). The interaction between year and colony was also included but only reported in the results table if the interaction was found to be significant. A Levene's test was conducted to ensure the assumption of equal variances was met. Residual plots were also found to be satisfactory after inspection for any abnormal patterns.

Foraging Tracks and Ranges

To filter out GPS co-ordinates not linked to foraging behaviour, only location points associated with dive events were exported to ArcMap (ESRI, 2019). ArcMap was used to make maps of foraging tracks for both Harrison and Moraine colonies over 2019 and 2020.

To make foraging ranges highlighting core areas of activity for each colony and year, it was first necessary to sub-sample each dataset on R, since the number of GPS fixes per bird varied greatly within and between colony/year. The number of fixes was chosen for each dataset that balanced equalizing the amount of representation from each bird while allowing total datapoint sample sizes from each colony to be as close to each other as possible across years. Birds from the Moraine colony in 2020 (n=5) were subsampled by taking 105 fixes per bird while birds from the Moraine colony in 2019 (n=6) were subsampled by taking 100 fixes per bird, although one bird from this year yielded only 29 fixes. This subsampling regime led to GPS fix sample totals of 525 for Moraine in 2020 and 529 for Moraine in 2019. Birds from the Harrison Cove colony in 2020 (n=8) were subsampled by taking 30 fixes per bird although one bird in this year only yielded 25 fixes while birds from Harrison Cove in 2019 (n=4) were subsampled by taking 45 fixes per bird, although one bird from this year yielded

only 7 fixes. This subsampling regime led to GPS fix sample totals of 235 for Harrison Cove in 2020 and 142 for Harrison Cove in 2019.

Kernel utilisation distributions (KUDs) were used to make foraging ranges for the subsamples of each colony and year, on R using the packages 'adehabitatHR' and 'sp.' Fixed KUDs failed to converge when choosing a bandwidth via the Least Squares Cross-Validation (LSCV) method and were estimated as much larger than the actual range using the "href" bandwidth method. Thus, KUDs were user-specified (Calenge 2019) with a smoothing factor of 0.015, selected by determining the value of h that represented the best balance between KUDs that were overestimations and KUDs that were unrealistically fragmented. Shapefiles of the 25%, 50%, 75% and 95% kernels were exported to ArcMap and mapped. The clipping tool was used in cases where there was slight overlap onto the land bordering the fiord. The 'calculate geometry' tool was used to calculate the area in km^2 for each kernel polygon per colony and year, and a table was created to display these. All maps made on ArcMap were projected on the New Zealand Transverse Mercator (NZGD 2000) co-ordinate system.

Comparison of dive data between years and colonies

Dive data were analysed with a custom-written script in Matlab 9. The dive analysis identified dive events for each individual and calculated several parameters for each dive, including duration, surface time, bottom time, number of wiggles, maximum depth and dive velocities in the ascent and descent phases. Bottom time was defined as the time spent at depths between 95% and 100% of the maximum depth (Mattern et al. 2013). 'Number of wiggles' denotes a pattern in dive profiles of small but rapid increases and decreases in depth that have often been used as an indicator of prey pursuit and foraging activity (Halsey et al. 2007). Dives were accepted by the software only if they passed the thresholds of 5 seconds for dive duration and 0.5 metres for dive depth, in order to exclude any non-diving, travelling behaviour and compensate for random pressure fluctuations when birds were at the surface. Following the methodology of Ydenberg & Clarke (1989), the dive parameter of 'dive efficiency' was computed as bottom time/(dive duration + post-dive interval) while 'foraging efficiency' was calculated as dive duration/(dive duration + post-dive interval).

Means and standard deviations were calculated to summarise the dive parameters for each colony over each year. Generalised Linear Mixed Models (GLMMs) and Linear Mixed Models (LMMs) fitted by a restricted maximum likelihood (REML) were used to determine

whether the year of the breeding season (2019/2020) and the colony site where individuals were from (Moraine/Harrison Cove) were influencing the dive behaviour of tawaki. Body mass was not included as a predictor variable in the models as no correlation was found between mass and key dive parameters such as dive depth and dive duration (see Appendix 1, Figure A1.1). Average body mass was also very similar across colonies and years (see Appendix 1, Table A1.1). To avoid pseudoreplication, a suitable random effects structure was included wherein trip identity was nested within bird identity to account for the differences between individuals, some of which had dive data collected from multiple foraging trips. Models with this structure were found to be the most parsimonious models based on their Akaike Information Criteria, tested using the 'anova' function. The year (2019/2020), colony (Moraine/Harrison Cove) and the interaction term (year*colony) were included as fixed effects. LMMs and GLMMs were fitted using the 'lmer' and 'glmer' functions in the 'lme4' package (Bates et al. 2015) in R (R Core Development Team 2021).

GLMMs were made for parameters with a non-normal distribution, whereas LMMs were fitted for parameters with normal distributions. Dive parameters that qualified as count data, such as number of dives, dives per hour and number of wiggles were analysed in GLMMs specified with a Poisson error structure. However, if these models were found to be over dispersed, they were refitted with a negative binomial error structure which was able to correct for overdispersion. GLMMs with a Gamma error structure were used for dive parameters that were always positive and/or positively skewed. For all models, the residuals were plotted and visually checked to ensure there were no signs of abnormal patterns or heteroscedasticity. Additionally, in the case of LMMs, the residuals were also checked for normality before approving the model. For both LMMs and GLMMs, Type II Wald chi square tests were used to assess the significance of the fixed effects and their interactions.

Dive parameters that were found to be significantly different between years or colonies were then explored at a finer scale to assess whether they were influenced by the hour of day and/or the maximum depth to which birds dived. A GLMM or LMM, was used depending on the response variable's distribution and after examining the normality of the residuals. For these models, the hour class and/or maximum dive depth were included alongside the explanatory variables of year and colony and the random effects of trip identity and bird identity. The model residuals were inspected for heteroscedasticity, and normality in the case of an LMM. Graphs were created in R to illustrate how significant response variables such as

dive number, depth, duration, descent velocity varied throughout the day. Further graphs were made to demonstrate the frequency distribution of dive depths when including one trip per bird, as well as the correlation between maximum dive depth and dive duration. To highlight the level of contrast between them, typical trip dive profiles of a fiord-foraging Harrison Cove bird and an ocean-foraging Moraine bird were displayed, alongside an example of a dive with wiggles. The relationship between depth class and the number of wiggles in a dive was graphed to determine whether the intensity of foraging activity varied across different depth classes.

Past research on other penguin species has split dive parameters into different categories for analysis based on whether individuals made long (>24 hours) or short (<24 hours) foraging trips (e.g., Carpenter-King et al. 2017). Very few Harrison Cove birds made long trips in 2019, and no birds made long trips in 2020 so these were not worth comparing. In 2019, a total of four individuals from Moraine made five long trips while four individuals made four short trips. In 2020, five long trips were recorded from three individuals while a total of eleven short trips were recorded from three individuals. Foraging efficiency was the only dive parameter that differed clearly between Moraine birds that made short (<24 hours) and long (> 24 hours) foraging trips (see Appendix 2, Figure A2.2). As the majority of dive parameters were not affected by the trip type of tawaki, dive parameters were not analysed separately between short and long trips.

Repeatability

The consistency of dive behaviours at both the population level and individual level was assessed through determining repeatability in dive parameters over consecutive trips during the breeding season for each bird. Thus, only birds that completed more than one foraging trip were included in this analysis. Using the ‘rptR’ package (Stoffel et al. 2017), the repeatability index (R), standard error, confidence intervals, and associated p-values were calculated for the dive parameters: dives per hour, maximum dive depth, dive duration, descent velocity, and ascent velocity. The LMM-based method was used to estimate repeatabilities (as described in Nakagawa & Schielzeth 2010) and a 95% confidence interval was calculated for each parameter based on 1000 bootstrapping runs. The model for the variables of dives per hour was performed using a Poisson error structure while the other parameters were performed using Gaussian error. For two of the Gaussian models, a

transformation was necessary to approximate normality - dive duration was square-root transformed, and maximum dive depth was log10 transformed. The LMM models included bird ID and trip ID as a random factor while year and colony were included as fixed factors to control for any differences between colonies or between years as might be a result of environmental variability. Non-adjusted repeatabilities (where the model includes rather than removes the phenotypic variance of the fixed effects) were chosen over adjusted repeatabilities (where the model removes the phenotypic variance of the fixed effects) as it was discovered that the fixed effects did not contribute significantly to the level of repeatability between and among the birds.

The 'rptR' package uses parametric bootstrapping to calculate confidence intervals, while applying randomization to generate p values. These two different methods are not always in perfect agreement. In some of the repeatability analyses, p values indicated significance despite the accompanying confidence interval including zero. In this case, it is best practise to interpret effect sizes together with confidence intervals. It follows that small repeatability estimates that also have a confidence interval that contains zero, do not truly suggest repeatability, even if the p value indicates significance. Significant repeatabilities larger than 0.1 can be considered as weak evidence, even if the confidence interval does include zero. In past work, consistency in dive behaviour has been considered high when $R > 0.50$, moderate when $0.25 < R < 0.50$ and low when $R < 0.25$ (Potier et al. 2015).

2.3 Results

2.3.1 Comparison of foraging behaviour between colonies and years

In 2019, foraging data were collected over ten foraging trips (seven of which were complete trips) from six tawaki in the Moraine colony in Milford Sound. Data was also collected over seven foraging trips (six of which were complete) from four tawaki in the Harrison Cove colony. Originally, two additional Harrison Cove birds were equipped with loggers but these malfunctioned and could not be used in the analysis. In 2020, dive data were collected from five Moraine birds and eight Harrison Cove birds which meant a total of 13 (out of 16) and 18 (out of 20) complete foraging trips, respectively.

Multiple foraging trip parameters were significantly different across years and between colonies. In 2019, birds from both Moraine and Harrison Cove went on significantly longer foraging trips than in 2020 and the trips made by Moraine birds were significantly longer than the trips made by birds from Harrison Cove (Table 2.1). No birds from Harrison Cove in 2019 made multi-day foraging trips and only 60% of trips from Harrison Cove tawaki occurred within the fiord, as compared to almost 90% of trips being fiord-based in 2020. Birds from both colonies travelled significantly greater maximum distances from their respective colony sites per trip in 2019 than 2020 and Moraine birds travelled further out from their colony than Harrison Cove birds (Table 2.1). The interaction between colony and year was found to have a significant effect on the cumulative distance travelled by tawaki, with birds from both colonies covering greater distances in 2019, and birds from Moraine travelling further than Harrison Cove tawaki (Table 2.1). There were no significant effects of the colony or year on the horizontal travelling speed of tawaki, however, birds did appear to be trending towards moving at slightly faster speeds in 2020 than 2019 (Table 2.1). Overall, the most notable differences in foraging behaviour occurred between Moraine and Harrison Cove birds in 2020, and between Harrison Cove birds across the years.

In 2019, 405 GPS locations from foraging tracks were obtained for Harrison Cove birds and 1547 from Moraine birds. In 2020, 2840 and 1033 locations were gathered from Moraine and Harrison Cove birds, respectively. These tracks revealed that in 2019, two of the four Harrison Cove birds exited the fiord to forage in the ocean whereas only one of the eight birds tracked exited the fiord to forage in 2020 (Figure 2.1). For Moraine tawaki, birds appeared to travel far out from their colony, into the ocean during both years, although foraging activity seemed more concentrated closer inshore in 2020 (Figure 2.1). These differences were also depicted in the kernel foraging ranges with Moraine birds having 25% and 50% KUDs that were concentrated more firmly in the coastal ocean in 2020 than in 2019 although the 75% and 95% KUDs extended further out into the open ocean (Figure 2.2). Moraine birds in 2020 spent 75% of their foraging trips within 20km from their colony site, compared to 2019 when the 75% kernel foraging range of Moraine tawaki extended about 47 km out from the colony (Figure 2.2). Steeper sections of bathymetry also seemed to correlate with core 25% and 50% KUDs (Figure 2.2). The foraging ranges of Moraine birds all decreased in area from 2019 to 2020, with the greatest difference in area occurring between the 75% KUDs across the years (Table 2.2).

For Harrison Cove birds, their kernel ranges in 2019 showed 95%, 75% and 50% cores of foraging activity occurring in the open ocean while in 2020, only the 95% KUD stretched outside the fiord while most of the foraging activity was centred within the fiord limits (Figure 2.3). In 2019, 25%, 50% and 75% kernel cores encompassed a wider area of the fiord than in 2020, although this might just be a function of the sample size being low in 2019 (Figure 2.3; Table 2.2). In 2020, 25% and 50% kernels cores were shifted further within the inner fiord, closer to the Milford Marina and the stretch of fiord outside Harrison Cove, whereas in 2019 these cores were more spread out, situated further down the fiord and encompassing Stirling Falls (Figure 2.3). The area of foraging kernels decreased dramatically for Harrison Cove birds between 2019 and 2020, especially so for the larger 95% range (Table 2.2). The magnitude of difference between the foraging areas of the colonies in 2020 is also clear, with the 50% kernel of Moraine birds being practically equivalent in size to the 95% foraging kernel of Harrison Cove birds (Table 2.2). In both years, the foraging ranges of Harrison Cove birds were consistently smaller than those of Moraine birds, however in 2019, Harrison Cove kernels ranged between 35%-73% the area of Moraine kernels, while in 2020 Harrison Cove kernels were only 10-20% the size of Moraine kernels (Table 2.2).

Table 2. 1 Summary of the attributes of tawaki tracked by year and colony as well as key foraging parameters with their mean ± standard deviation and corresponding results of the ANOVA test performed. Degrees of freedom were 1,19. Only complete trips were used and if a bird completed more than one full trip, trips were averaged to obtain one trip per bird for analysis. A log10 transformation was used for the trip duration and maximum distance from colony per trip, while a natural log transformation was used for distance travelled per trip.
* data from five 2019 Harrison Cove birds was available for the parameter of trip duration (h)

	2019		2020		ANOVA Output			
	Moraine	Harrison Cove	Moraine	Harrison Cove	Predictors	F value	P value	Effect Size
Number of birds	6	4*	5	8	-	-	-	-
Number of trips	7	6	13	18	-	-	-	-
Number of trips >24hr	5	2	5	0	-	-	-	-
Percentage of trips in fiord only (%)	0	60	6	89	-	-	-	-
Foraging parameters								
Trip duration (h)	31 ± 14	22 ± 11	25 ± 13	11 ± 4	Colony	7.7	<0.05	0.28
					Year	4.8	<0.05	0.19
Max. distance from colony per trip (km)	29.6 ± 9.2	26.3 ± 21.1	23.5 ± 13.2	7.7 ± 8.9	Colony	10.1	<0.005	0.35
					Year	7.0	<0.05	0.27
Distance travelled per trip (km)	74.4 ± 28.1	66.1 ± 40.8	66.5 ± 31.8	19.5 ± 11.1	Colony	17.5	<0.001	0.39
					Year	7.1	<0.05	0.27
					Colony*Year	4.4	<0.05	0.19
Travelling speed ($km\ h^{-1}$)	0.94 ± 0.10	1.00 ± 0.21	0.82 ± 0.10	0.87 ± 0.20	Colony	0.6	0.43	<0.01
					Year	3.4	0.08	0.15

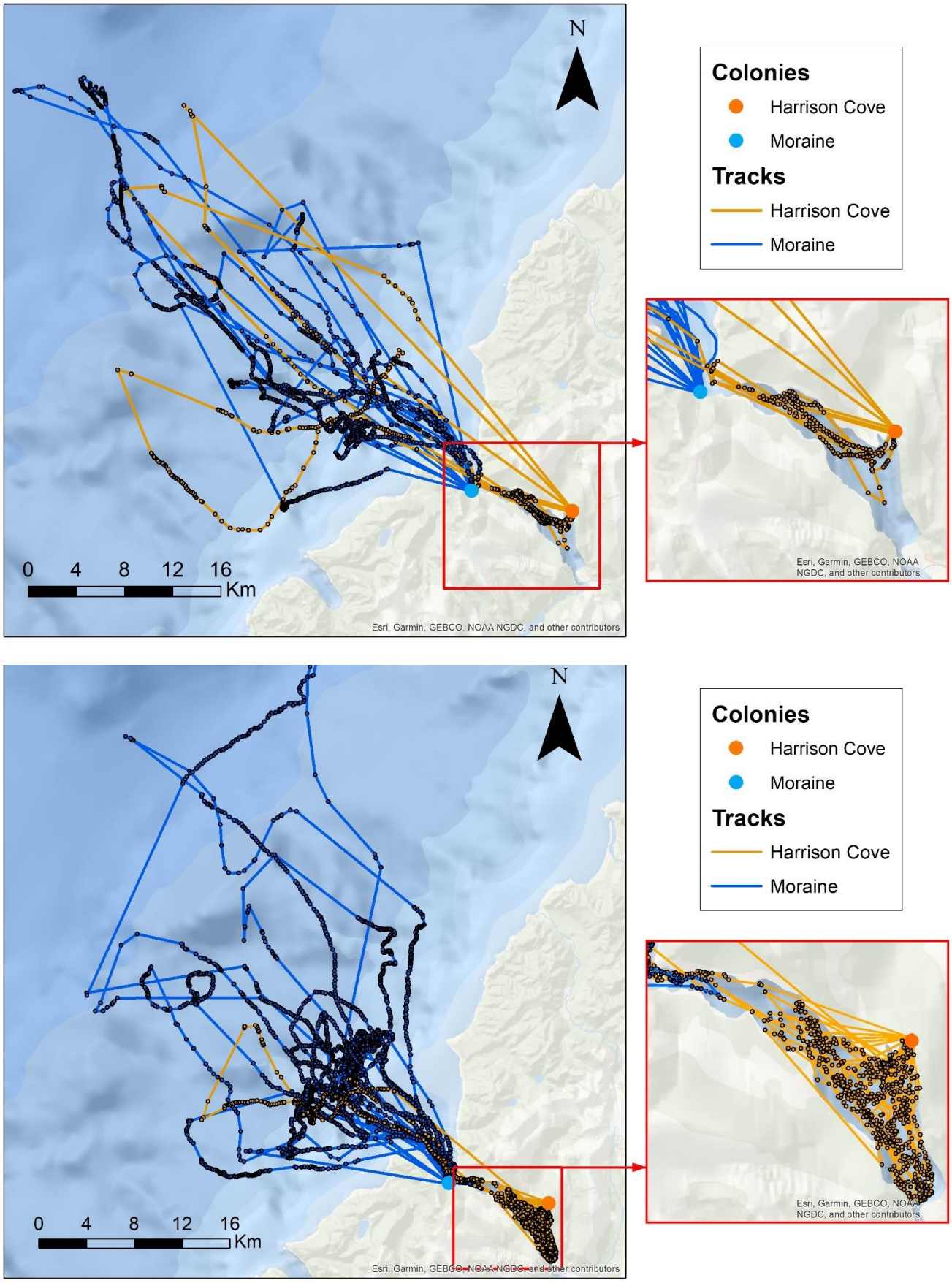

Figure 2.1 Map depicting the raw GPS points and foraging tracks of tawaki from the Harrison Cove and Moraine colonies in Milford Sound during guard stage of the 2019 (top) (n = 10) and 2020 (bottom) (n = 13) breeding seasons. Fiord area is outlined (right).

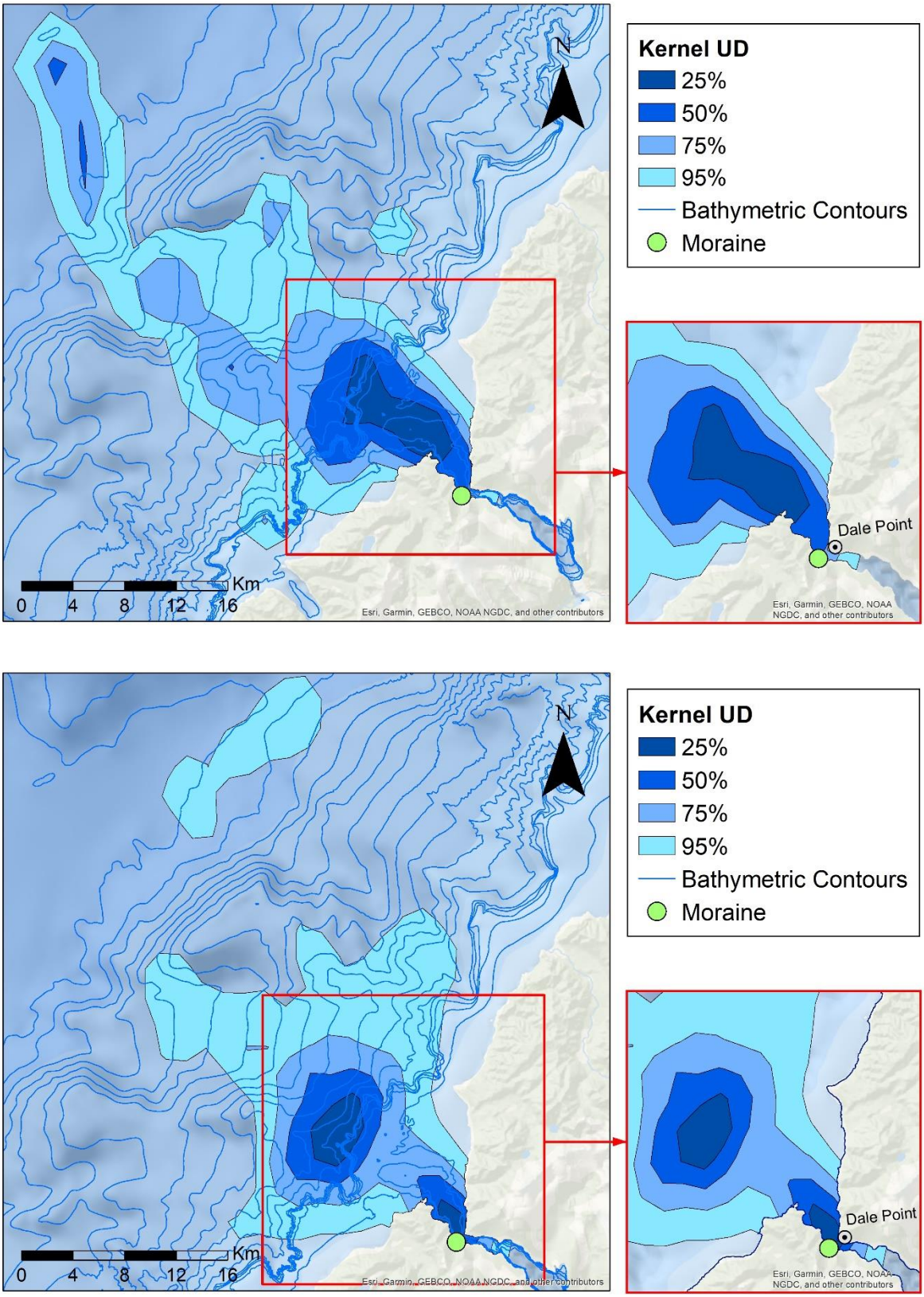

Figure 2.2 Map depicting the 25%, 50%, 75% and 95% foraging kernels of tawaki from the Moraine colony in Milford Sound during guard stage of the 2019 (top) (n = 6) and 2020 (bottom) (n = 5) breeding seasons. Close up of the core foraging area is outlined with Dale Point labelled (right). Blue lines represent NIWA bathymetry contours (2016). Contour interval is 250m in depths greater than 200m and 50m in depths less than 200m.

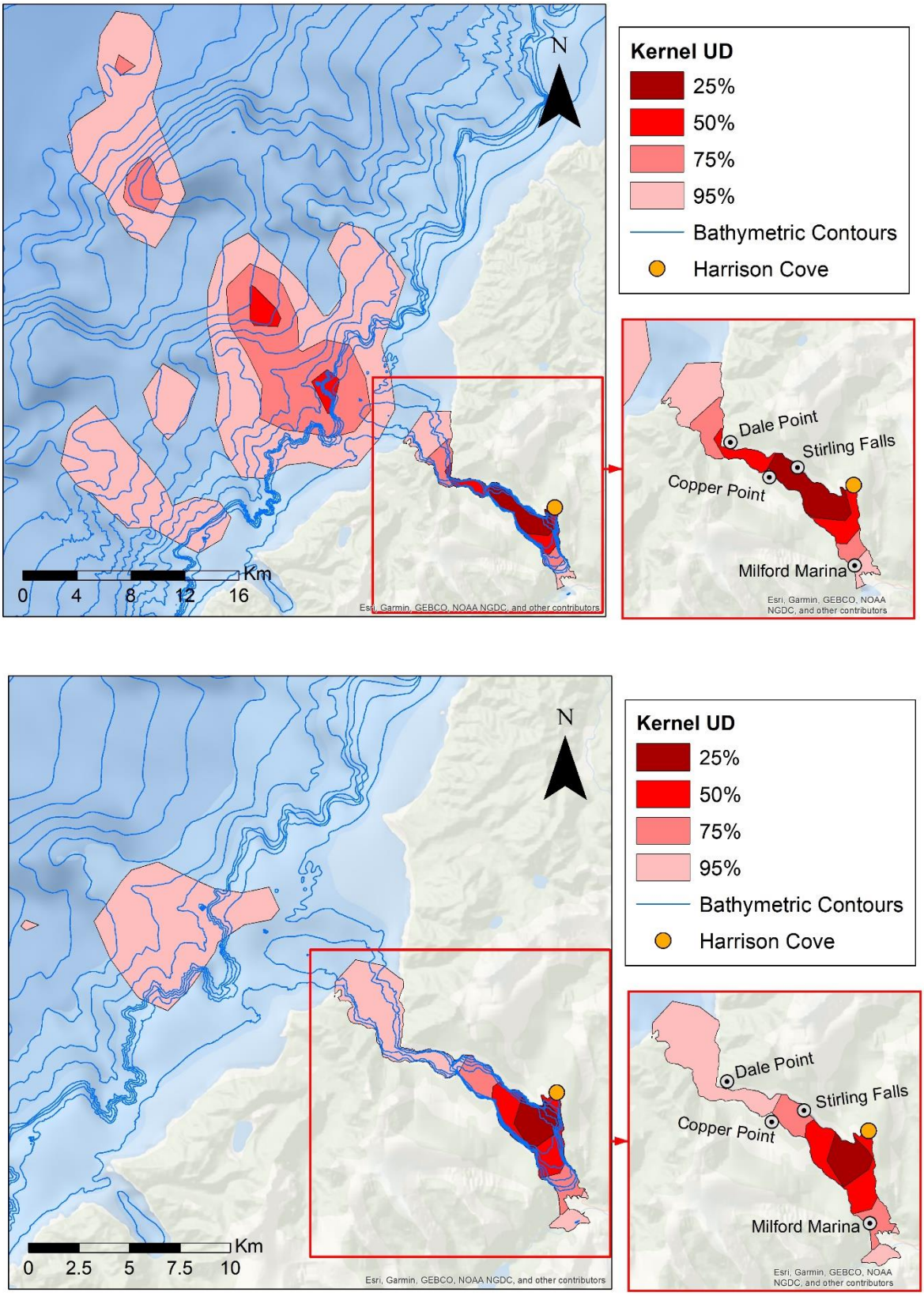

Figure 2.3 Map depicting the 25%, 50%, 75% and 95% foraging kernels of tawaki from the Harrison Cove colony in Milford Sound during guard stage of the 2019 (top) (n = 4) and 2020 (bottom) (n = 8) breeding seasons. Fiord area is outlined with key locations labelled (right). Blue lines represent NIWA bathymetry contours (2016). Contour interval is 250m in depths greater than 200m and 50m in depths less than 200m.

Table 2. 2 Area (km^2) of 25%, 50%, 75% and 95% foraging kernels, calculated from a subsample of GPS points collected from tawaki foraging from the Moraine and Harrison Cove colonies in Milford Sound during guard stage of the 2019 and 2020 breeding seasons.

Colony	Year	Area 25%	Area 50%	Area 75%	Area 95%
Harrison Cove	2019	7.83	22.3	104	386
Moraine	2019	30.2	86.4	244	531
Harrison Cove	2020	3.77	9.76	14.5	64.9
Moraine	2020	19.5	62.3	143	451

2.3.2 Comparison of dive behaviour between colonies and years

A total of 10,111 diving events were recorded for Moraine tawaki in 2019 and 9,154 in 2020. For Harrison Cove tawaki, a total of 5,161 dive events were recorded in 2019 and 7,573 in 2020.

There were no significant differences between the years or colony sites in the number of dives per hour, number of wiggles per dive, time spent at the bottom, time spent at the surface, or the ascent rate (see Appendix 2, Figure A2.1). Despite this, bottom time did appear to trend close to significance with respect to year, with birds tending to spend longer periods of time at 95-100% of their maximum dive depth in 2020 than in 2019 (see Appendix 2, Figure A2.1).

Dive frequency and timing

Although there was no significant effect of colony or year on the number of dives per hour, differences were apparent at a finer scale, with respect to how dive activity changed throughout the course of a day, dependent on the hour.

The hour of day was found to significantly influence the number of dives that occurred (GLMM, $\chi^2 = 7.97$, P = <0.005; $\chi^2 = 76$, P = <0.001). In 2019, birds from both Harrison Cove and Moraine displayed a similar pattern wherein the number of dives peaked at the start of the day – at 9am for Moraine and between 8am-12pm for Harrison Cove, before decreasing markedly from 1pm-6pm and peaking again at the end of the foraging trip around 7-8pm (Figure 2.4). The dive rate for Moraine birds in 2019 remained consistently high, around 50 dives per hour between 8am-12pm before decreasing sharply whereas the number of dives for

2019 Harrison Cove birds decreased gradually from the peak of 60 dives at 9am to a low of around 25 dives at 1pm. The lower frequency of dives between 1-6pm was more consistent for Harrison Cove birds than for Moraine birds who had a slightly more erratic pattern of dive frequencies through the course of the day (Figure 2.4).

In contrast, Harrison Cove birds in 2020 did not have nearly as much of a dip in dive frequencies between 1-5pm as they did 2019, and the peak in dive number at 9am was also less clear (Figure 2.4). Overall, the hourly dive frequencies of Harrison Cove birds in 2020 was much more uniform and ranged between an average of 35-45 dives per hour (Figure 2.4). Meanwhile, Moraine birds in 2020 maintained a more distinct pattern of dive frequencies than in 2019, with a peak at 6am before decreasing in frequency until a low at 1-2pm followed by an increase until a further peak at 6pm (Figure 2.4). Peak dive frequencies for Moraine in 2020 tended to be between 35-45 dives per hour while their lowest frequency hour class of 2pm yielded an average of only 17 dives per hour (Figure 2.4). Overall, Harrison Cove birds appeared to dive more often at each hour in 2020 than in 2019, although their peak frequencies were greater in 2019 than 2020 (Figure 2.4). On the other hand, Moraine birds dived at relatively lower frequencies per hour in 2020 than in 2019 (Figure 2.4).

Dive depth & dive duration

The interaction between the year and the colony site a bird was from was found to be significant for dive duration and maximum dive depth (Table 2.3). Birds from the Moraine colony appeared to have longer dive durations in 2020 than in 2019, whereas birds from Harrison Cove dived for shorter periods of time in 2020 compared to 2019 although this difference from year to year was not as markedly different as for the Moraine birds (Table 2.3). Similarly, birds from Moraine dived to significantly deeper depths in 2020 than in 2019 whereas the birds from Harrison Cove dived to deeper depths in 2019 than in 2020 (Table 2.3). Harrison Cove birds dived significantly deeper than Moraine birds in 2019 but this reversed in 2020 with Harrison Cove birds diving to shallower depths than Moraine birds (Table 2.3).

Moraine birds appeared to begin making deeper dives earlier on in the day in 2020 than in 2019 and they also sustained this pattern of deeper diving more consistently throughout the course of the day (Figure 2.5). In comparison, Harrison Cove birds concentrated most of their dives in the 0-25m section of the water column and dived deeper more often in 2019 than

2020 (Figure 2.5). While Moraine birds had high densities of dives in the upper 0-30m of the water column, they also had relatively high densities of dives concentrated between the depths of 60-90m (Figure 2.5). When the dive depth distributions of Harrison Cove birds were compared with their location ‘within the fiord’ or ‘outside of the fiord’ taken into account, it was found that almost all dives greater than 70m took place on foraging trips that birds made outside the fiord (Figure 2.6).

In 2020, a substantial 85% of dives made by Harrison Cove birds were in the upper 0-20m of the water column while just over half (51%) of dives made by Moraine birds were within this depth range (Figure 2.7). In comparison, Moraine birds in 2019 made 70% of their dives to maximum depths of 0-20m whereas 2019 Harrison Cove birds made shallow dives less often, with only 56% of their maximum dive depths falling within 0-20m (Figure 2.7). Moraine birds dived deeper more often in 2020 compared to 2019, with 35% of their 2020 dives occurring over depths of 50m whereas just 10% of their 2019 dives were greater than 50m (Figure 2.7). For Harrison Cove, the trend was the opposite where about 3% of their dives were deeper than 50m in 2020 but 26% of dives took place at greater depths than 50m in the year prior (Figure 2.7).

The hour of day had a significant effect on the maximum dive depth (LMM, $\chi^2 = 15.5$, P = <0.001). The interaction between the three variables of hour of day, colony and year was also significant ($\chi^2 = 172$, P = <0.001) indicating a varying effect on maximum dive depth over the hours of the day depending on the year and the colony site. In 2019 the distribution of dive depths throughout the course of the day was skewed to the left with dives increasing in depth from 9am onwards for Harrison Cove birds before peaking in maximum depth at 4pm and decreasing in depth into the evening (Figure 2.8). Dive depths through the course of the day for Moraine birds in 2019 followed a similar pattern of peaking in depth around the late afternoon although it was more erratic and less pronounced (Figure 2.8). In 2020, however, Moraine birds had a highly symmetrical distribution where dives steadily increased in depth from 5am and peaked between the hours of 12pm-3pm before becoming increasingly shallower by each hour into the evening (Figure 2.8). In 2020, the hourly average depth distribution for Harrison Cove birds was almost uniform throughout the entire day from 6am to 6pm and this was markedly different to their 2019 Harrison Cove counterparts, as well as to Moraine birds (Figure 2.8).

Maximum dive depth was found to be strongly correlated with dive duration at both colonies and for both years (Figure 2.9). While the correlations between mean dive depth and mean dive duration were very similar over both years for Harrison Cove birds, 2020 individuals from Moraine had mostly higher mean dive durations and deeper mean dive depths than their 2019 counterparts (Figure 2.9).

The hour of day had a significant effect on the dive duration (LMM, $\chi^2 = 84.7$, P = <0.001). The interaction between the three variables of hour of day, colony and year was also significant ($\chi^2 = 44.1$, P = <0.001), indicating a differential effect on dive durations over the hours of the day depending on both the year and the colony site. During the course of the day, the mean dive durations varied substantially for Harrison Cove birds in 2019 and less so for Moraine birds in 2019 (Figure 2.10). However, this trend was reversed in 2020 as Harrison Cove birds retained relatively consistent dive durations of about 70 seconds from pre-dawn to the end of the foraging trips in the early evening (5am -7pm) (Figure 2.10). This aligns with the consistency apparent in the mean maximum dive depths that the 2020 Harrison Cove birds foraged at across the day (Figure 2.8). In contrast, Moraine birds in 2020, had mean dive durations that increased steadily during the morning and settled at around 120 seconds between 10am-4pm before decreasing towards evening (Figure 2.10). In 2019, peaks in mean dive durations were also present for Moraine but they were more subtle and occurred later in the day between 1-5pm at just over 80 seconds (Figure 2.10). The Harrison Cove birds in 2019 also had mean dive durations that peaked in the late afternoon around 3-4pm although these dive durations were much longer at just under 125 seconds (Figure 2.10).

Descent velocity

There was a significant interaction present between the year and the colony for the dive parameter of descent velocity (Table 2.3). Moraine birds had greater descent velocities in 2020 than in 2019 whereas Harrison Cove birds had slower descent velocities in 2020 than 2019 (Table 2.3). Harrison Cove birds had significantly faster descent velocities than Moraine birds in 2019 whereas in 2020 Harrison Cove birds had slower descent velocities than Moraine birds (Table 2.3).

The hour of day had a significant effect on the descent velocity (LMM, $\chi^2 = 214.5$, P = <0.001). The interaction between the three variables of hour of day, colony and year was also significant ($\chi^2 = 101.2$, P = <0.001) indicating a differing effect on descent velocity over the

hours of the day depending on both the year and the colony site. In 2019, the descent velocities of both colonies appeared to climb irregularly throughout the day with Harrison Cove birds reaching a peak descent velocity at 4pm while peak velocities occurred for Moraine birds at 2-3pm and 6pm (Figure 2.11). The year of 2020 was a different story, where the distributions of mean descent velocities appeared very similar for both colonies, with descent velocities being less erratic and more evenly spread throughout the day (Figure 2.11). Descent velocity appeared to slowly but steadily increase from 6am-10am for Harrison Cove birds while this increase is much steeper for Moraine birds as they settled at a higher average descent velocity (Figure 2.11). The hour of peak velocity for Moraine birds in 2020 was at midday with an afternoon dip occurring at 1pm, while the peak hour for Harrison Cove birds was at 10am with an afternoon dip occurring at 2pm (Figure 2.11). Moraine birds in 2019 had a pronounced drop in descent velocities over the hours of 6pm to 8pm whereas in 2020, Moraine birds did not decrease their average descent velocity so sharply towards the end of their foraging trips in the evening (Figure 2.11).

Comparing the average descent velocity to the depth class at which a bird was foraging at revealed how descent velocity tended to increase with maximum dive depth (see Appendix 2, Figure A2.2). In 2020, birds from Moraine reached an average of 1.2 m/s 10 metres earlier compared to 2019, in the 20-30m depth class and this is the class at which descent velocities of Moraine and Harrison Cove birds began to diverge with Harrison Cove birds, settling at slower velocities at each depth class than Moraine birds until they reached depths of 90+ metres (see Appendix 2, Figure A2.2).

Foraging efficiency and number of wiggles

The year significantly influenced the foraging efficiency of tawaki with foraging efficiency being higher in 2020 than in 2019 (Table 2.3). There was no significant effect of colony site on foraging efficiency (Table 2.3). The hour of day also had no significant effect on the foraging efficiency (LMM, $\chi^2 = 0.08$, $P = 0.776$). However, the interaction between the three variables of hour of day, colony and year was significant ($\chi^2 = 36.0$, $P = <0.001$) indicating a differing effect on foraging efficiency over the hours of the day dependent on the year and colony site. This was particularly evident at the Moraine colony where foraging efficiencies varied noticeably throughout the day, although the nature of this variation was different between years (Figure 2.12). In 2020, the foraging efficiencies of Moraine birds decreased

from 6am to 2pm before increasing between 2pm-5pm (Figure 2.12). The foraging efficiencies of Moraine birds in 2019 decreased from 6am to 8am and remained relatively constant throughout the morning-afternoon before rising again in the evening (Figure 2.12). The foraging efficiencies of Moraine birds in 2019 were noticeably lower in the morning (8am-11am) compared to 2020 Moraine birds. For Harrison Cove birds in 2019, their foraging efficiencies only experienced a decrease from the early morning until 10am and remained relatively constant through midday to evening while their 2020 counterparts maintained an almost completely stable level of foraging efficiency throughout all the daylight hours (6am-7pm) (Figure 2.12).

Although the number of wiggles did not significantly differ between colonies or over the two years, a trend was present with 2020 birds appearing to have a slightly higher numbers of wiggles per dive than in 2019 (Table 2.3). The number of wiggles provides an indication of the foraging activity occurring and allows some discernment between travelling or non-foraging dives that have a smooth V-shaped dive profile and foraging dives (Figure 2.13c). The number of wiggles per dive from Harrison Cove birds in 2019 was greater than the number of wiggles from Moraine birds in the 30-70m depth profiles, suggesting that Harrison Cove birds were more actively foraging in this depth range than were Moraine birds (Figure 2.14). These differences between the colonies in number of wiggles were not so notable in 2020, however, Moraine birds in 2020 made noticeably more wiggles in their deeper dives of 90-100+ metres than in 2019, indicating that prey pursuits were more common at these depths in 2020 than 2019 (Figure 2.14).

Given the noticeably lower number of wiggles at 0.5-10m, it is likely that most dives occurring in this depth category were travelling dives (Figure 2.14). This is supported by the shallow dives visible at the beginning and end of a foraging trip for the typical Moraine bird as first they tended to commute to foraging grounds outside the fiord before making deeper dives for feeding (Figure 2.13a). This is also clear in the other parameters, where Moraine birds dive to shallower depths, have slower descent velocities, shorter dive durations and higher foraging efficiencies during the early morning and late evening of their foraging trips as they are likely travelling (Figure 2.8; Figure 2.10; Figure 2.11; Figure 2.12). For Harrison cove birds, it is possible that both foraging and travelling dives occur in the upper 0.5-10m of the water column as the dive profile for the trip of a typical fiord-foraging Harrison Cove bird

included most dives taking place in the upper 5-20m of the water column, with the occasional deeper dive interspersed throughout (2.13b).

Foraging efficiency was the only dive parameter that differed clearly between Moraine birds that made short (<24 hours) and long (> 24 hours) foraging trips (see Appendix 2, Figure A2.2). In 2019 the foraging efficiency of Moraine birds was only slightly higher on long trips than on short trips but in 2020 foraging efficiency was strikingly higher during long trips (see Appendix 2, Figure A2.2). Furthermore, all three individuals making long trips had similarly high foraging efficiencies with hardly any variation between them (see Appendix 2, Figure A2.2).

Table 2. 3 Summary table displaying the mean and standard deviations of key dive parameters for tawaki from the Moraine and Harrison Cove colonies in Milford Sound during the guard stage of the breeding season in years 2019 and 2020. Means were calculated using the average of individual means. Model parameters are also displayed for either the Linear Mixed Model (LMM) or a Generalised Linear Mixed Model (GLMM) used to determine whether the predictors of colony, year or the interaction between colony and year were significant. P values in bold are under the set significance level of <0.05, df = 1.

	2019		2020				
	Moraine	Harrison Cove	Moraine	Harrison Cove	Predictors	X^2 value	P value
Number of birds	6	4	5	8	-	-	-
Dive parameters							
Dive duration (s)	63.4 ± 38.6	77.0 ± 42.3	87.0 ± 48.5	74.2 ± 37.7	Colony	1.28	0.258
					Year	1.11	0.293
					Colony*Year	5.15	**<0.05**
Max. dive depth (m)	18.2 ± 17.0	24.7 ± 20.6	30.1 ± 28.1	16.3 ± 11.8	Colony	6.67	**<0.01**
					Year	0.19	0.659
					Colony*Year	11.93	**<0.001**
Descent velocity (ms^{-1})	0.85 ± 0.38	0.94 ± 0.38	1.05 ± 0.43	0.86 ± 0.32	Colony	5.63	0.018
					Year	2.33	0.127
					Colony*Year	11.03	**<0.001**
Foraging efficiency	0.37 ± 0.17	0.38 ± 0.15	0.40 ± 0.17	0.42 ± 0.17	Colony	3.57	0.06
					Year	12.13	**<0.001**
					Colony*Year	0.72	0.40
Number of wiggles per dive	7.6 ± 5.8	8.3 ± 5.9	9.1 ± 6.6	8.7 ± 5.6	Colony	0.02	0.90
					Year	2.87	0.09
					Colony*Year	0.23	0.63

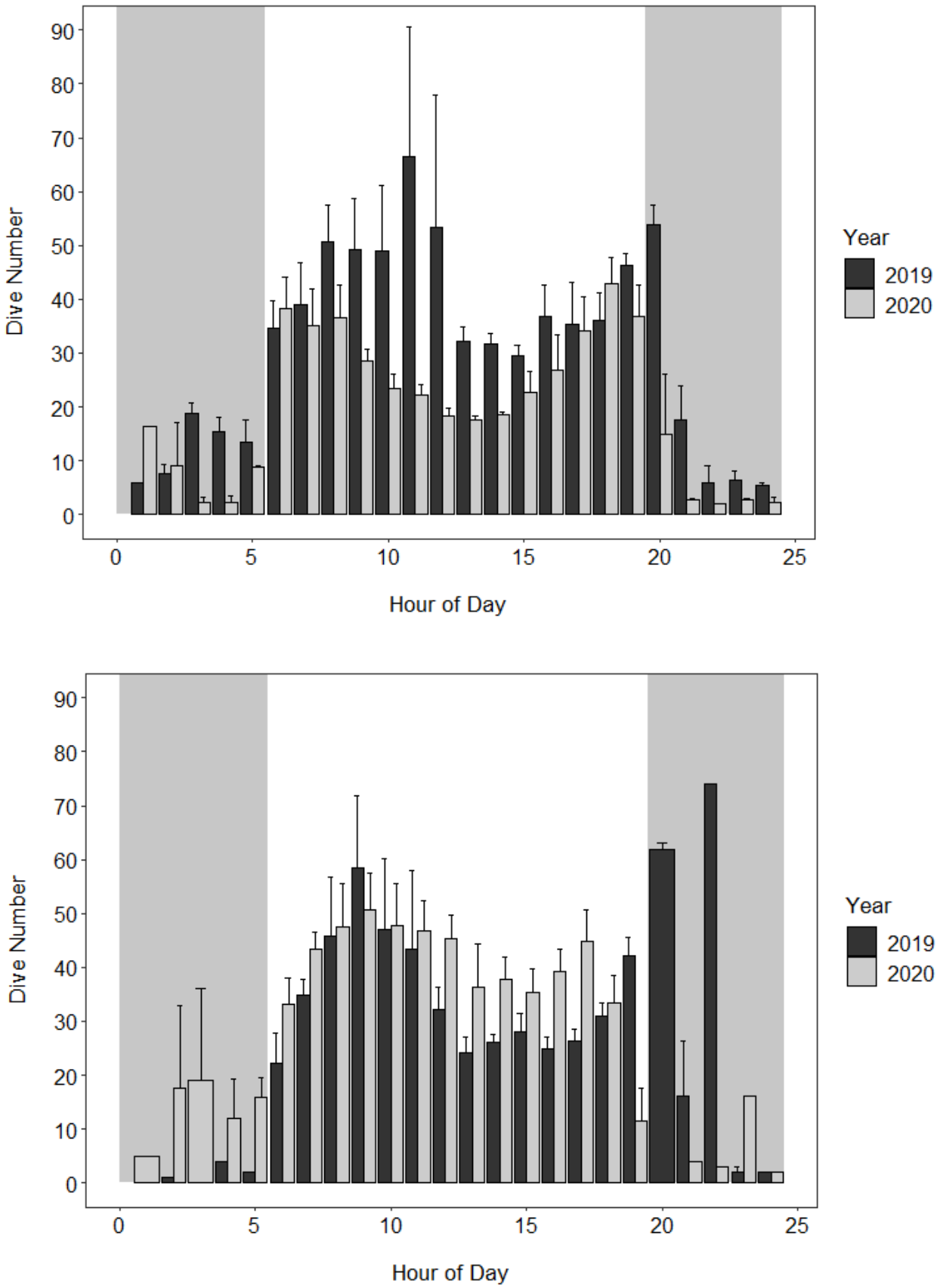

Figure 2.4 Average number of dives (± standard error) across the hours of the day for tawaki from two colonies in Milford Sound, Moraine (top) and Harrison Cove (bottom) during the guard stage of the breeding season in years 2019 and 2020. Harrison Cove: n = 4 (2019), n = 8 (2020); Moraine: n = 6 (2019), n = 5 (2020). Grey areas represent night-time.

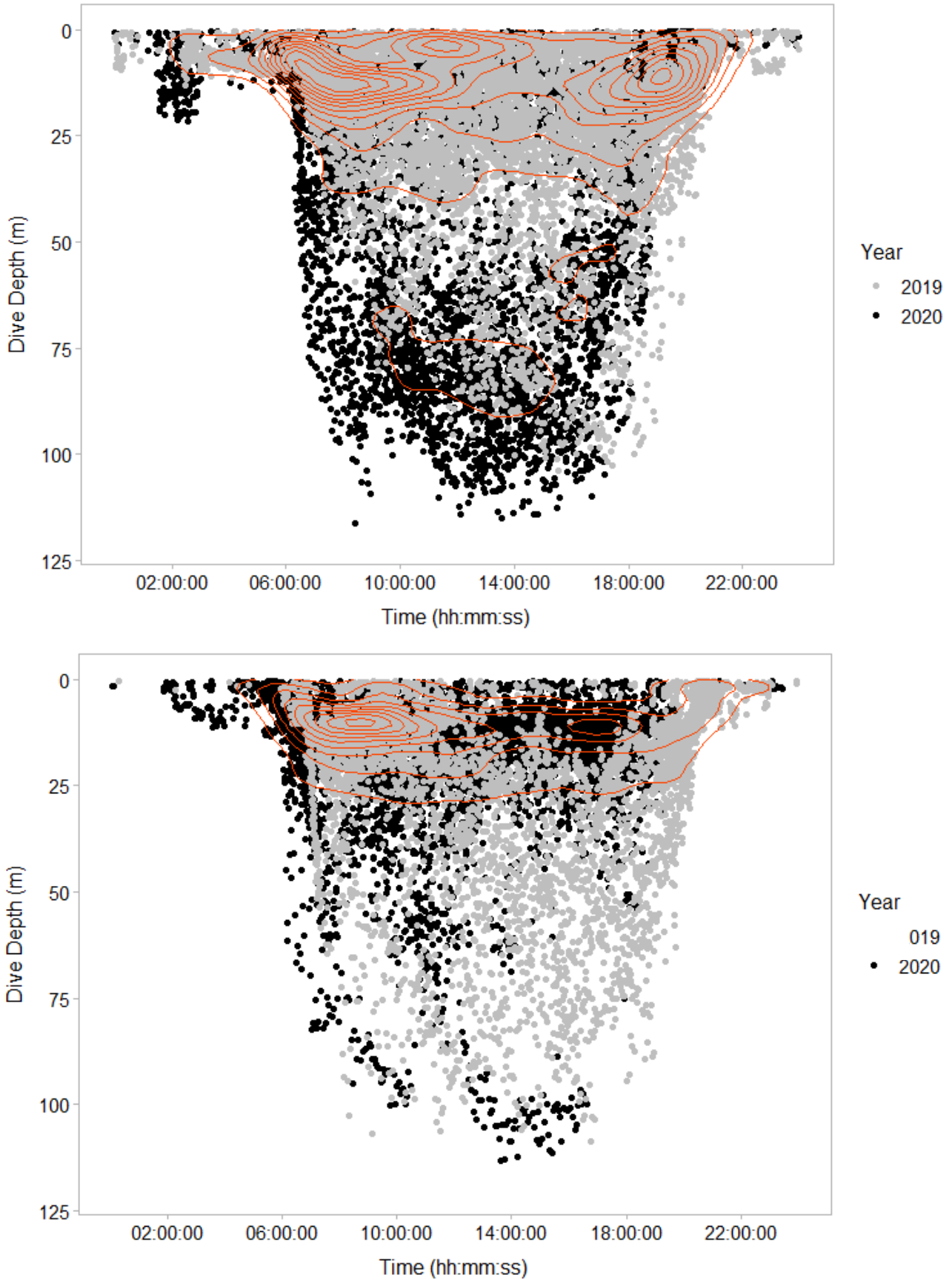

Figure 2.5 Maximum depth of the dives made by tawaki from two colonies in Milford Sound: Moraine (top) (n = 19265) and Harrison Cove (bottom) (n = 12734) throughout the day during the guard stage of the breeding seasons of 2019 and 2020. Harrison Cove: dive events = 5161, n = 4 (2019), dive events = 7573, n = 8 (2020); Moraine: dive events = 10111, n = 6 (2019), dive events = 9154, n = 5 (2020). 2D kernel density function displays the areas of highest density (plotted in orange contours).

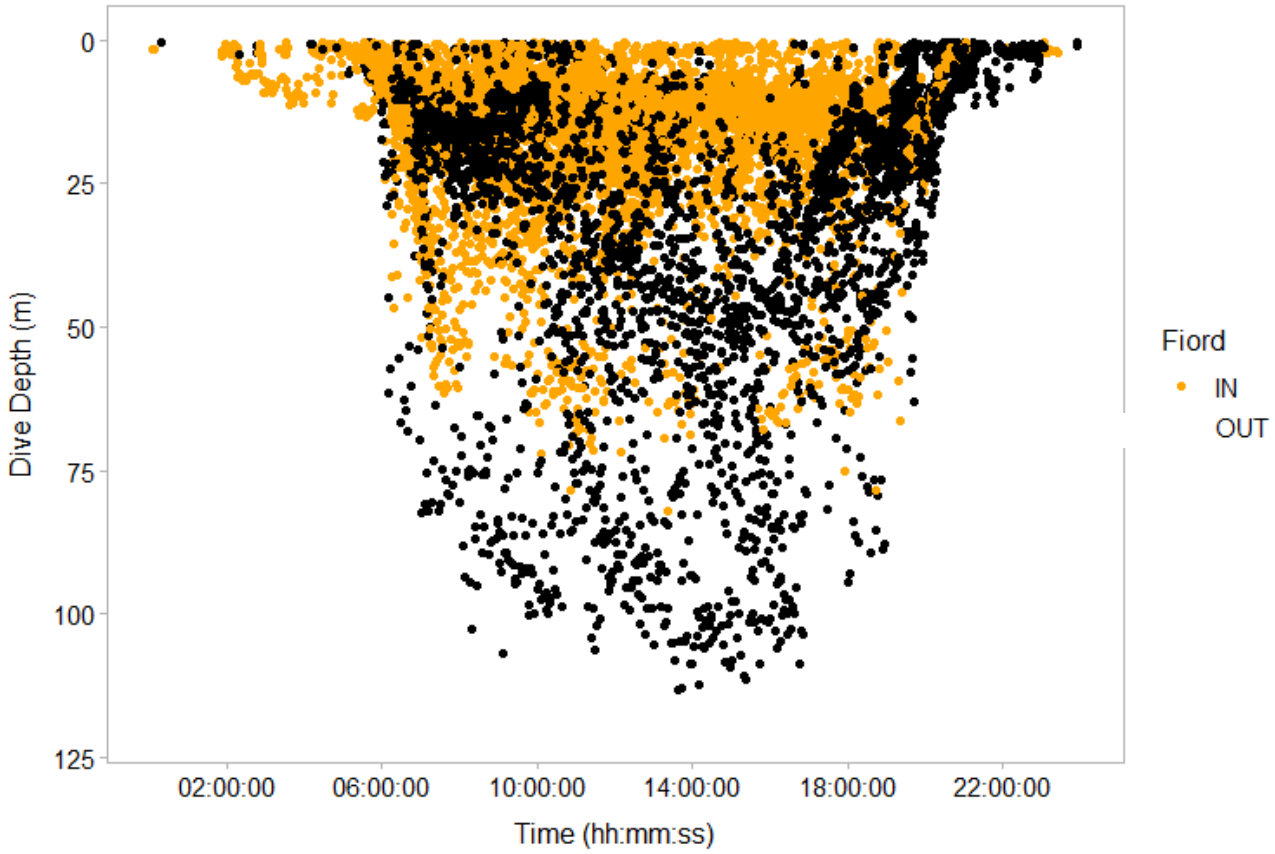

Figure 2.6 Maximum depth of the dives within the fiord (dive events = 7748; n = 8) and out of the fiord (dive events = 4078; n = 3) made by tawaki from Harrison Cove throughout the day during the guard stage of the breeding seasons of 2019 and 2020.

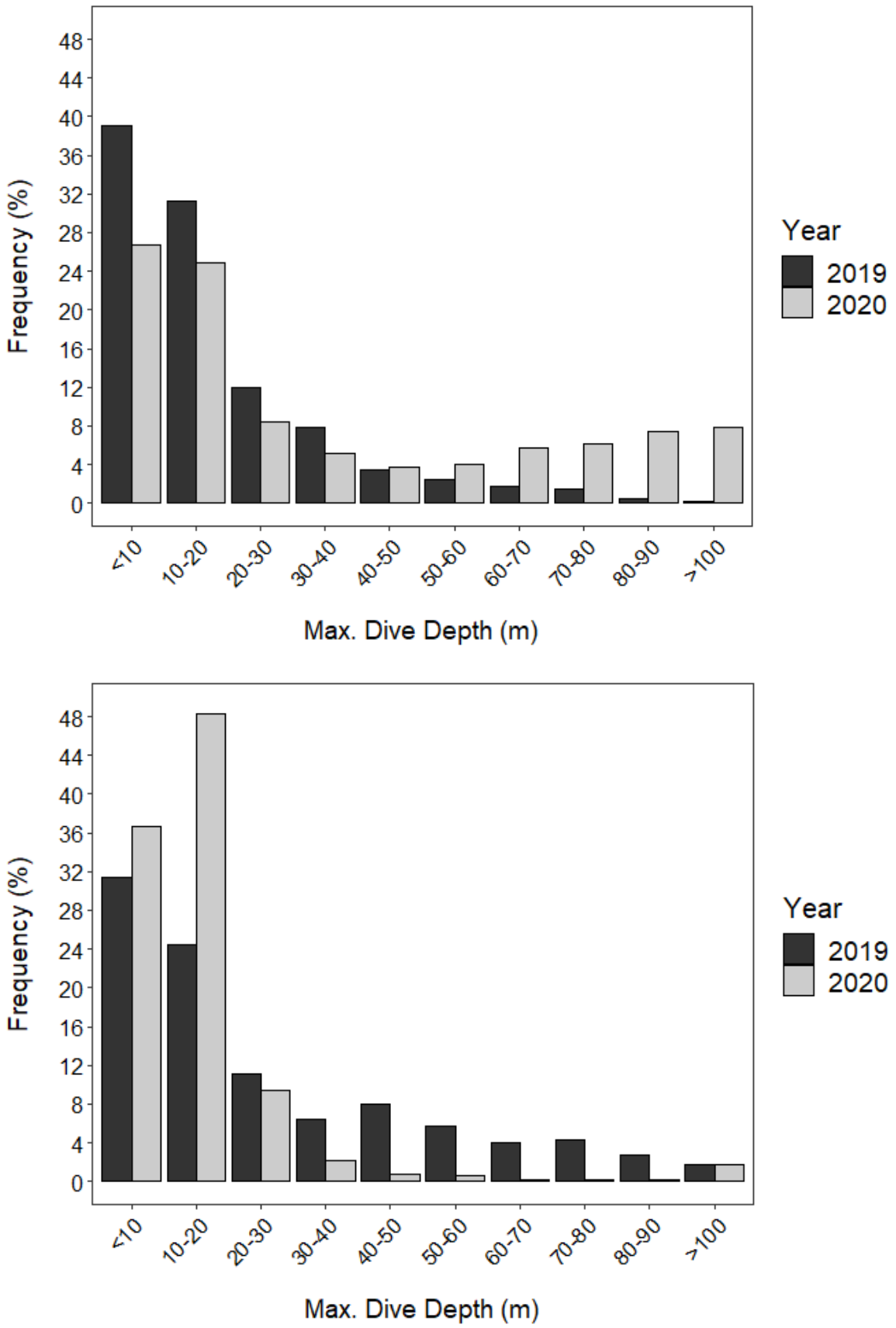

Figure 2.7 Frequency distribution of maximum dive depths for tawaki from Moraine (top) and Harrison Cove (bottom) during the guard stage of the 2019 and 2020 breeding seasons. Only the 1st trip of each individual is used, to avoid any bias in the distribution towards individuals who completed multiple trips. Harrison Cove: dive events = 4100, n = 4 (2019) dive events = 3190, n = 8 (2020); Moraine: dive events = 6519, n = 6 (2019), dive events = 3129, n = 5 (2020).

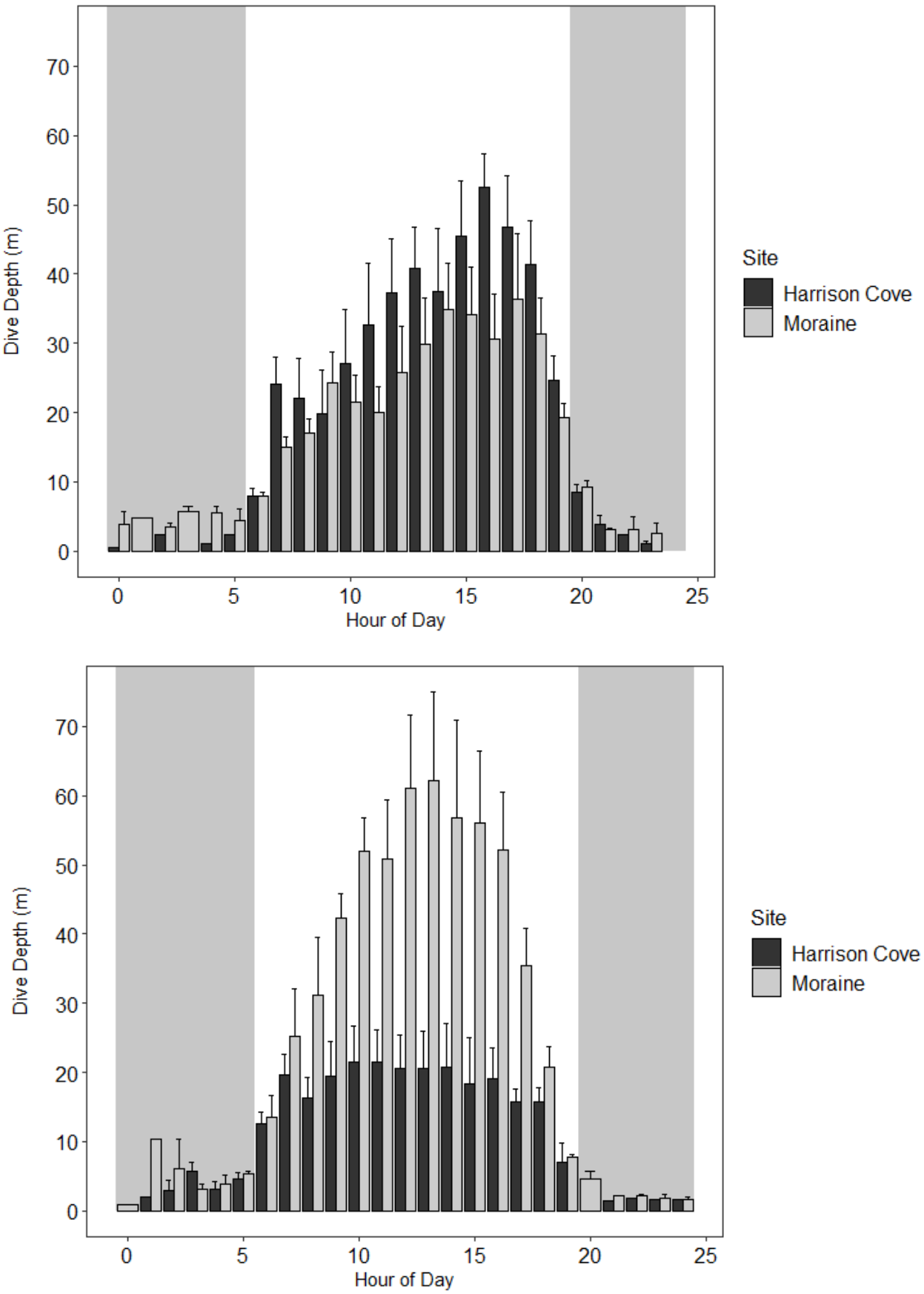

Figure 2.8 Average maximum dive depths (± standard error) across the hours of the day for tawaki from the Moraine and Harrison Cove colonies in Milford Sound during the guard stage of the breeding season in years 2019 (top) and 2020 (bottom). Harrison Cove: n = 4 (2019), n = 8 (2020); Moraine: n = 6 (2019), n = 5 (2020). Grey areas represent night-time.

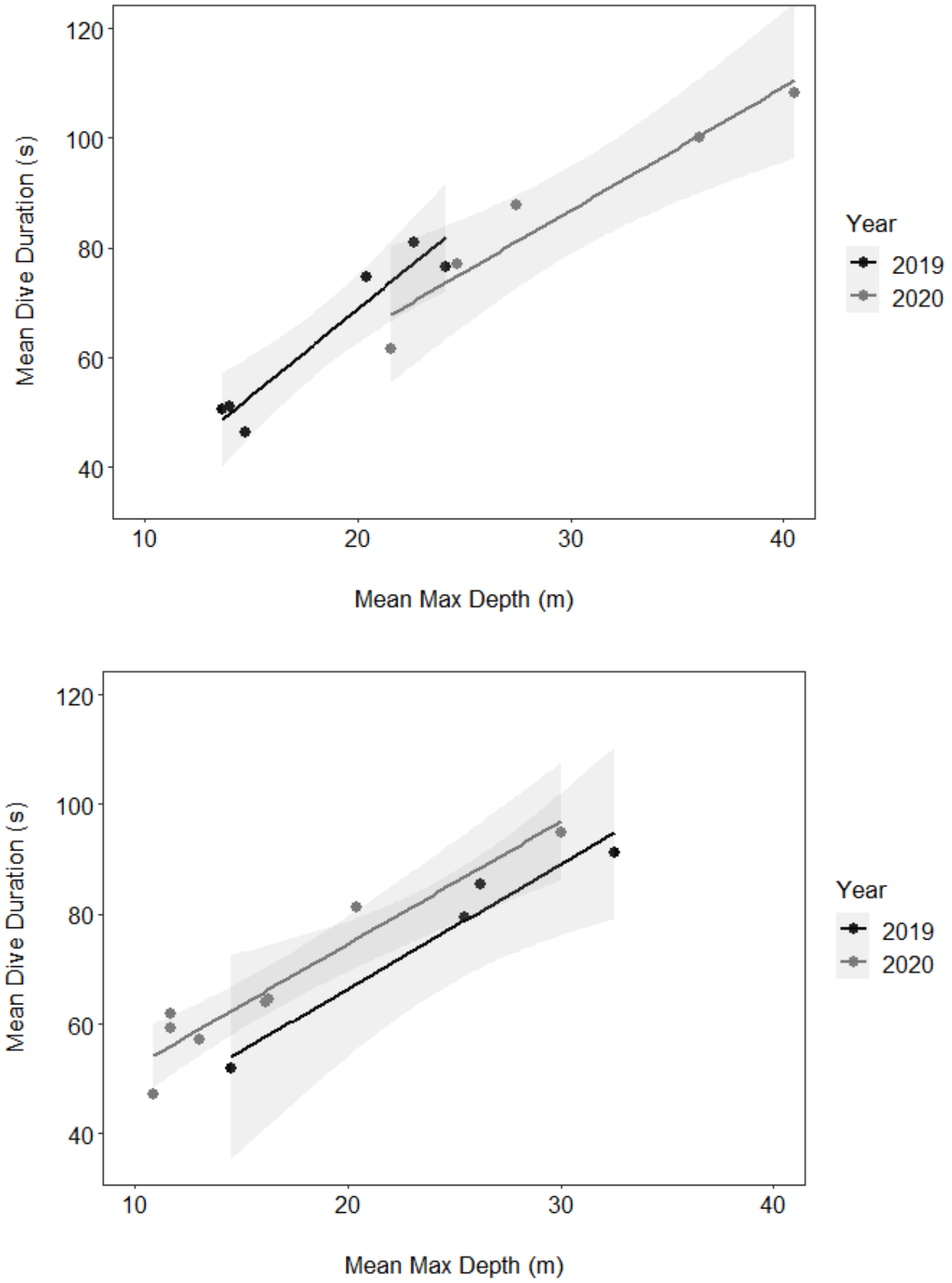

Figure 2.9 Correlative relationship between the mean dive duration and mean maximum depth for individual tawaki from two colonies in Milford Sound: Moraine (top), and Harrison Cove (bottom) during the guard stage of the 2019 and 2020 breeding seasons. Moraine: 2019 $r^2 = 0.91$, 2020 $r^2 = 0.93$. Harrison Cove: 2019 $r^2 = 0.95$, 2020 $r^2 = 0.91$. Harrison Cove: n = 4 (2019), n = 8 (2020); Moraine: n = 6 (2019), n = 5 (2020).

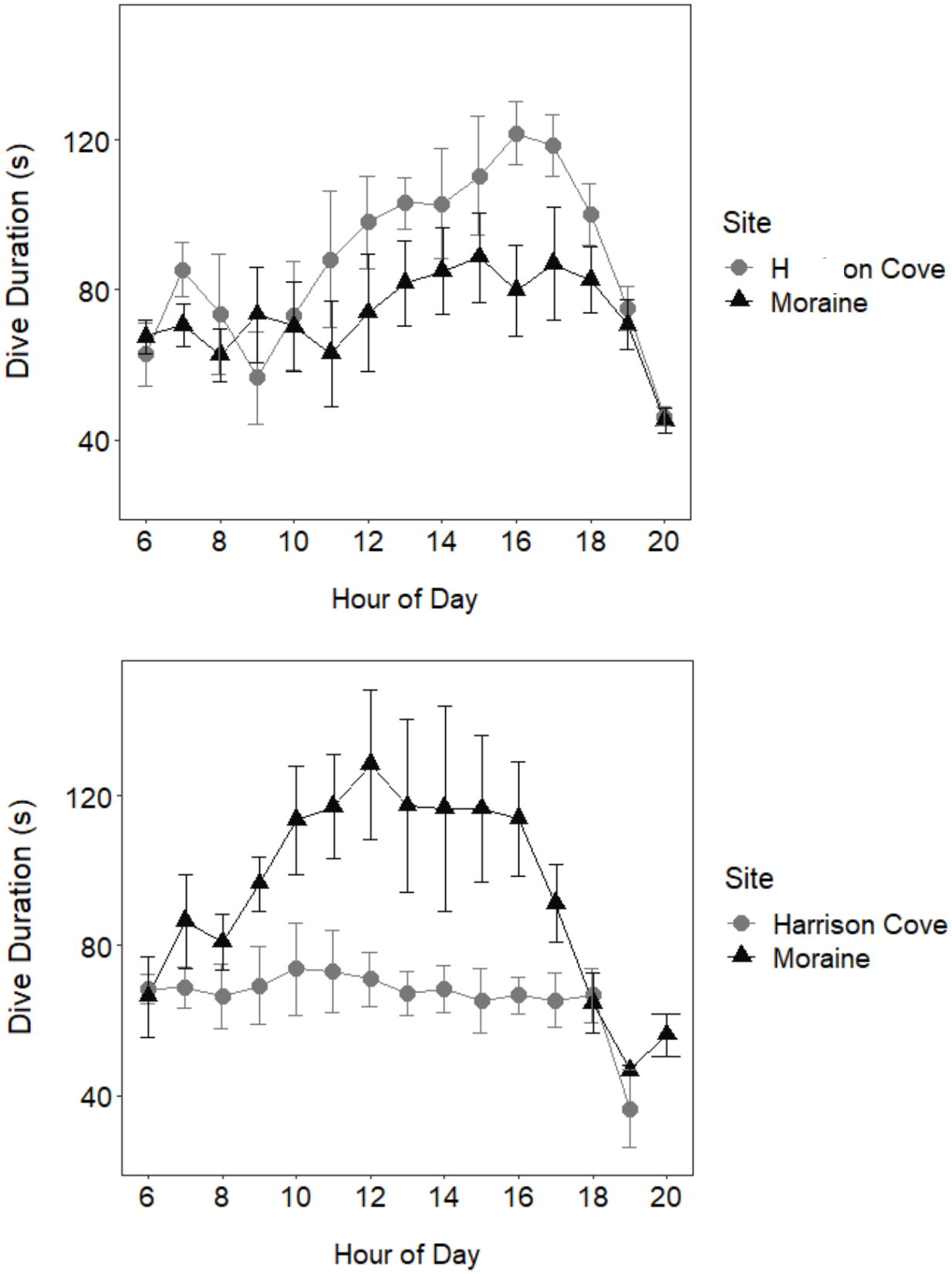

Figure 2.10 Comparison of mean dive durations (±standard error) at each hour of the day for tawaki from two colonies in Milford Sound (Moraine and Harrison Cove), during the guard stage of the 2019 (top) and 2020 (bottom) breeding seasons. Harrison Cove: n = 4 (2019), n = 8 (2020); Moraine: n = 6 (2019), n = 5 (2020).

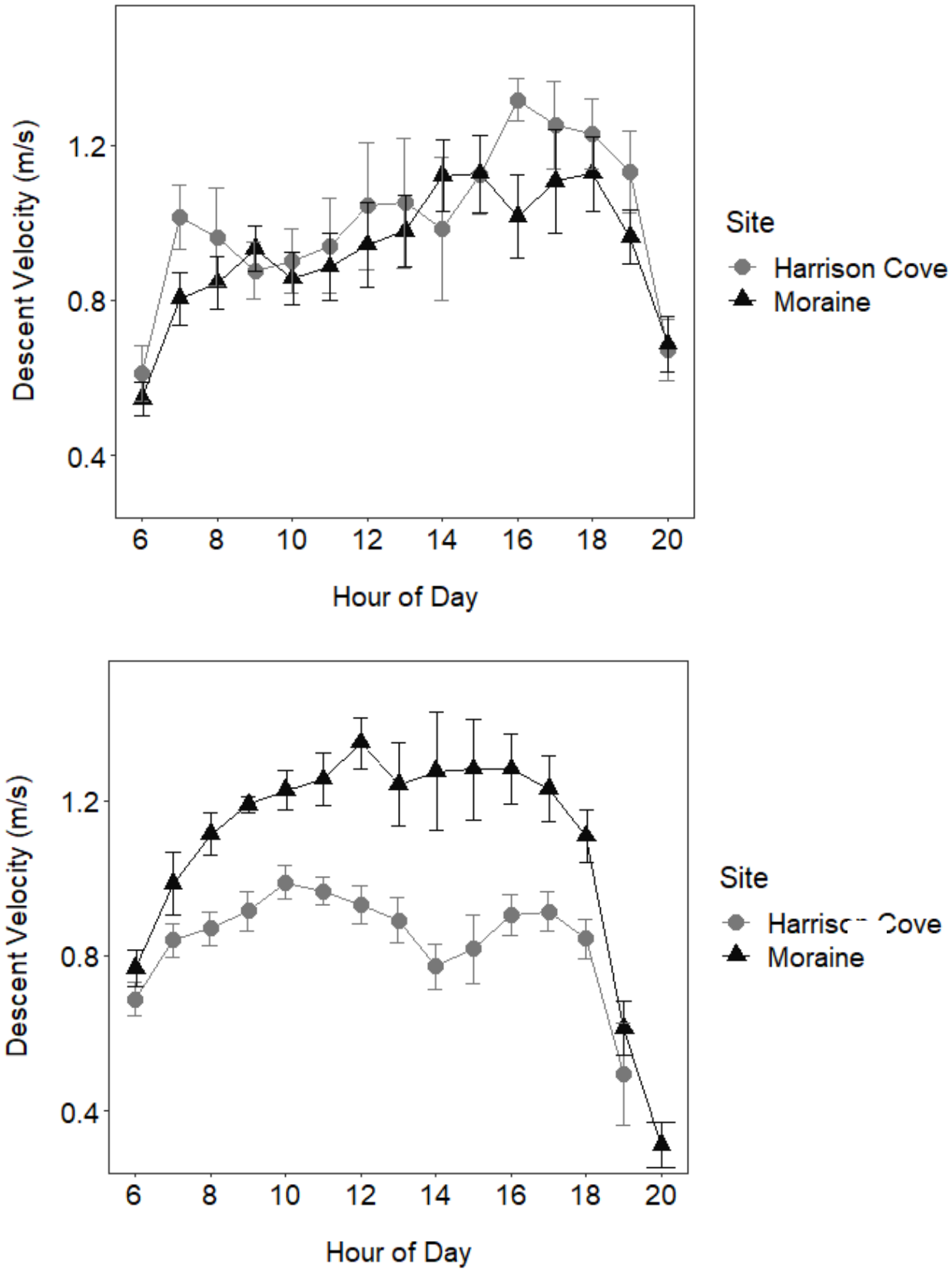

Figure 2.11 Comparison of mean descent velocities (±standard error) at each hour of the day for tawaki from two colonies in Milford Sound (Moraine and Harrison Cove), during the guard stage of the 2019 (top) and 2020 (bottom) breeding seasons. Harrison Cove: n = 4 (2019), n = 8 (2020); Moraine: n = 6 (2019), n = 5 (2020).

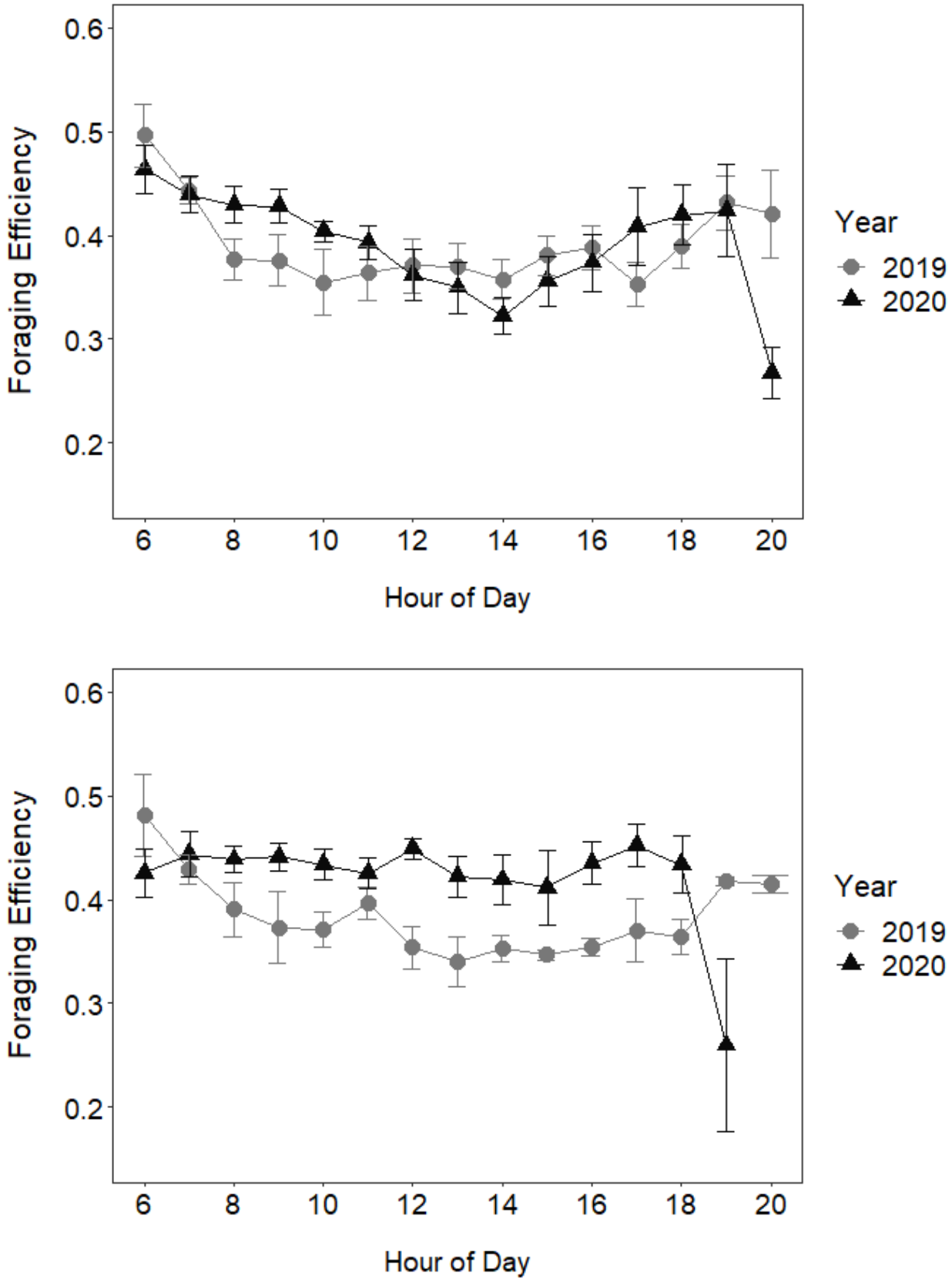

Figure 2.12 Comparison of mean foraging efficiency (±standard error) at each hour of the day for tawaki from two colonies in Milford Sound: Moraine (top) and Harrison Cove (bottom), during the guard stage of the 2019 and 2020 breeding seasons. Harrison Cove: n = 4 (2019), n = 8 (2020); Moraine: n = 6 (2019), n = 5 (2020).

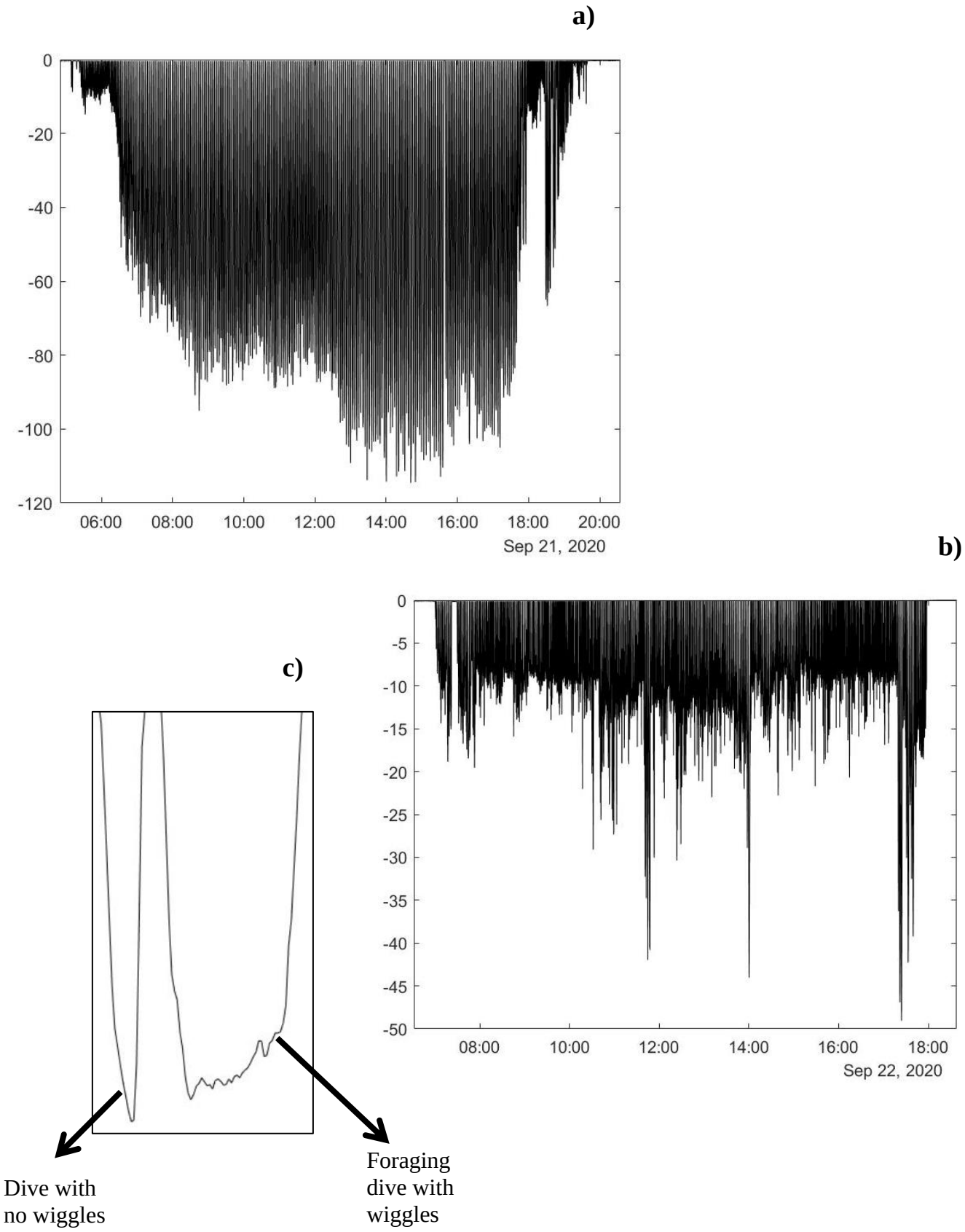

Figure 2.13 Diagram of the dive profile of a typical tawaki from **a)** Moraine (2020) throughout one full trip **b)** Harrison Cove (2020) throughout one full trip and **c)** diagram of isolated dives that are representative of a non-foraging or travelling dive with no wiggles and a foraging dive with multiple wiggles.

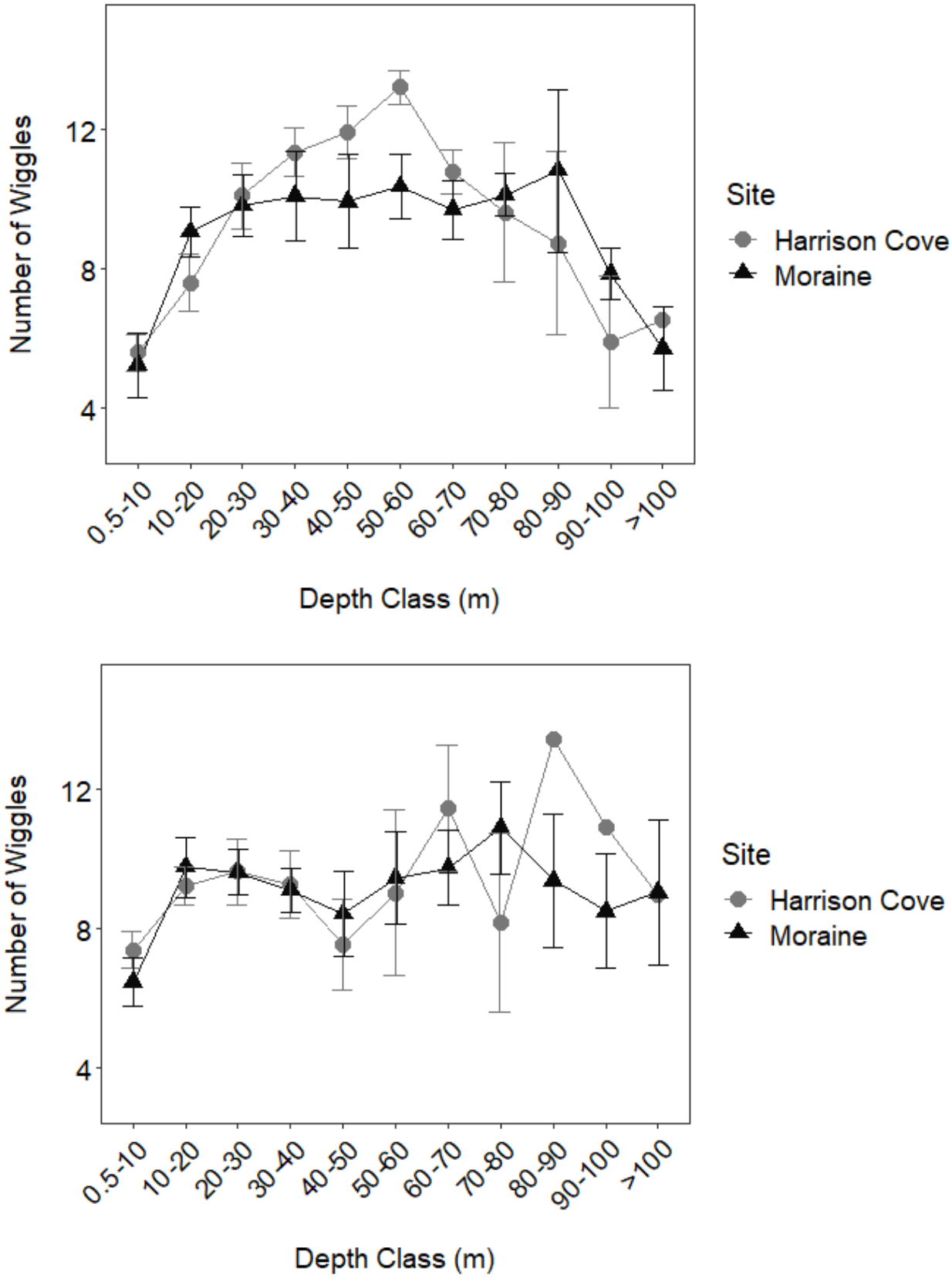

Figure 2.14 Comparison of mean number of wiggles (±standard error) at depth classes of 10m intervals for tawaki from two colonies in Milford Sound (Moraine and Harrison Cove), during the guard stage of the 2019 (top) and 2020 (bottom) breeding seasons. Harrison Cove: n = 4 (2019), n = 8 (2020); Moraine: n = 6 (2019), n = 5 (2020).

2.3.3 Individual Repeatability

Individual tawaki appeared to be highly flexible and show low repeatability in their dive behaviours, although there was generally statistically lower repeatability among individuals (when Bird ID was the grouping factor) than within individuals (when Trip ID was the grouping factor) (Table 2.4). Dives per hour, maximum dive depth, dive duration, descent velocity and ascent velocity all had low repeatabilities over multiple trips per individual, and the low level of repeatability for these parameters was statistically significant (Table 2.4). The only dive parameter with a significantly low level of repeatability among birds was dive duration (Table 2.4). Although dives per hour, maximum dive depth and descent velocity were indicated to have significantly low repeatabilities among birds, this is unreliable as their confidence intervals all still included zero (Table 2.4).

Table 2. 4 Summary table of the results from repeatability tests to determine the level and significance of repeatability within individuals, between multiple trips (shown with the grouping factor "Trip ID"), as well as between individuals (shown with the grouping factor "Bird ID"). Samples sizes: individuals = 16, trips = 46, dive events = 19,835.

	Trip ID				Bird ID			
	R	SE	CI (lwr, upr)	P	R	SE	CI (lwr, upr)	P
Dives per hour	0.105	0.039	0.038, 0.185	**<0.001**	0.098	0.047	0, 0.177	**<0.05**
Max dive depth (m)	0.179	0.042	0.102, 0.261	**<0.001**	0.093	0.056	0, 0.212	**<0.05**
Dive duration (s)	0.138	0.034	0.078, 0.212	**<0.001**	0.133	0.061	0.019, 0.252	**<0.01**
Descent velocity (ms^{-1})	0.161	0.038	0.089, 0.231	**<0.001**	0.088	0.053	0, 0.207	**<0.05**
Ascent velocity (ms^{-1})	0.108	0.023	0.062, 0.149	**<0.001**	0.009	0.016	0, 0.054	0.3

2.3.4 Summary comparison with tawaki from Open Bay Island

There are a few noticeable differences when the dive and foraging parameters of Milford Sound tawaki are compared to those from tawaki tracked at Open Bay Island – the only other study to publish tawaki dive data thus far. The mean trip duration of birds from the Moraine colony was markedly longer than birds from Harrison Cove and Open Bay Island and Moraine birds made trips travelling the longest horizontal distances (Table 2.5). On average, birds from Moraine also foraged further out from their colony location although there was a

greater range of maximum distances travelled by Open Bay Island birds (Table 2.5). The dive frequency of Moraine birds was lower than Open Bay Island birds while the dive frequency of Harrison Cove birds was notably higher, potentially due to Harrison Cove tawaki diving more often at shallower depths than birds from other colonies. Both the average depth and duration of dives by birds from the Milford Sound colonies appeared to be similar to birds from Open Bay Island, however, birds from Milford Sound tended to spend less time at the surface in between dives. The ascent and descent rates of birds from both Milford Sound colonies were consistently higher at $0.9ms^{-1}$ than those from Open Bay Island birds at $0.6ms^{-1}$.

Table 2. 5 Summary table comparing past research on the foraging and dive parameters of guard stage tawaki from Open Bay Island (Poupart et al. 2019) with tawaki from the Moraine and Harrison Cove colonies in Milford Sound. Parameters given are means with ranges in parentheses where possible while * denotes mode and $^{+}$ denotes a mean of the modes. Samples sizes: Open Bay Island: individuals = 23, trips = 25, dive evets = 23172. Moraine: individuals = 11, trips = 20, dive events = 19265. Harrison Cove: individuals = 12, trips = 25, dive events = 12734.

Parameters	**Open Bay Island**	**Moraine**	**Harrison Cove**
Trip duration (h)	17 (8-41)	28 (13-65)	15 (3-40)
Max. distance from the colony (km)	25 (11-134)	27 (3-51)	15 (3-47)
Total horizontal distance travelled (km)	56	71	36
Dive frequency (h^{-1})	23*	19*	33*
Dive depth (m)	22^{+}	24	20
Duration (s)	74^{+}	77	71
Post-dive interval (s)	19^{+}	14	13
Ascent rate (ms^{-1})	0.6	0.9	0.9
Descent rate (ms^{-1})	0.6	0.9	0.9

2.4 Discussion

2.4.1 Differences in spatial foraging behaviour between colonies and years

GPS tracks were examined to determine if the foraging movements of tawaki varied between an outer-fiord colony (Moraine) and inner-fiord colony (Harrison Cove) across two consecutive seasons. Tawaki showed clear polarity in their spatial use and foraging trip parameters between colonies, with the most striking differences occurring in the 2020 breeding season when almost all Harrison Cove tawaki foraged within the fiord while Moraine birds foraged in the open ocean. The negligible overlap between the foraging ranges of 2020 Moraine and Harrison Cove birds might be a due to inherited spatial foraging preferences based on the colony they were born at or partially as a result of foraging segregation between colonies. Multiple past studies have revealed how neighbouring penguin colonies of the same species mitigate intra-specific competition for resources by spatially segregating across available foraging grounds (Hoskins et al. 2008; Sánchez et al. 2018; Gulka et al. 2020). A recent review investigating overlap between colony foraging spaces reported that foraging segregation occurred in 79% of the 39 studies examined, which included 24 different seabird species (Bolton et al. 2019). Although there appears to be a high prevalence of inter-colony segregation in seabirds, complete segregation within obvious boundary lines are rare and usually there is some degree of partial overlap (Bolton et al. 2019; Ito et al. 2021). This was true for Moraine and Harrison Cove birds as in both years, as one-to-two Harrison Cove birds made foraging trips out into the open ocean, overlapping with the foraging territory of Moraine birds. However, there was only one instance of a Moraine bird foraging within the outer fiord area and zero cases of Moraine birds foraging in the inner fiord, past Copper Point. This suggests that there might be somewhat of a boundary beyond which Moraine birds do not forage within the inner fiord, where the highest intensity of foraging from Harrison Cove birds takes place.

It is some wonder that no Moraine birds forage extensively within the fiord when it appears to be a productive foraging habitat, especially for Harrison Cove birds in 2020, which had significantly shorter trip durations, and foraging distances than Moraine birds. The commuting costs for Moraine birds are significantly higher as they tend to travel out to the ocean before beginning their foraging bouts whereas Harrison Cove birds begin foraging almost as soon as they reach the water outside their colony. Similar behaviour has been

observed in murres (*Uria aalge*) breeding at a large offshore and a small inshore colony, where birds from the offshore colony travelled greater distances with more time spent commuting but it was hypothesised that this cost was balanced out by the benefit of reaching predictable and abundant aggregations of prey (Gulka et al. 2020).

Numerous studies have supported the initial prediction by Ashmole (1963) that the exploitation of prey resources in the waters surrounding seabird colonies leads to the formation of a 'halo' of reduced food availability. Generally, the larger the size of the colony, the more substantial is the extent of prey depletion (Gaston et al. 2007; Jovani et al. 2016). Moraine is a much larger colony than Harrison Cove, and it is possible that the birds from Moraine are contributing to a 'halo' effect in the coastal ocean, which makes it more profitable for Harrison Cove birds, and other smaller inner-fiord colonies, to forage closer to their respective colony sites and remain within the fiord (Ito et al. 2021). This has been found in multiple past studies where larger colonies constrain the foraging ranges of smaller colonies (Ainley et al. 2004; Ito et al. 2021). Ainley et al. (2004) discovered that while little foraging area overlap existed between a large penguin colony and smaller colonies, the foraging ranges of smaller colonies overlapped significantly, and this would be an interesting concept to test out with the other smaller inner-fiord tawaki colonies that exist in Milford Sound (Mattern & Long 2017).

The extent of foraging segregation might also alter depending on the degree of prey abundance across breeding seasons (Lynnes et al. 2002). This may explain why more Harrison Cove birds foraged in the coastal ocean in 2019 than in 2020 – either the food resources within the fiord were beginning to be depleted or the oceanic prey was particularly abundant. It is unlikely however, that the latter case is true, considering Moraine birds exerted greater foraging effort further out from the colony in 2019 than 2020, suggesting that local prey availability was lowered in 2019, driving tawaki to increase their search areas and trip durations to encounter prey (Weavers 1992). In both 2019 and 2020, Moraine birds did seem to return to a particular area of the coastal ocean, characterised by steeper bathymetric features, suggesting that there may be some reliable foraging patches, even if prey availability changes across years. Even when two colonies are using the same foraging space, they are still able to create ecological segregation in their foraging behaviour by diving at different times in the day or concentrating dives at different depths of the water column (Wilson 2010; Cimino et al. 2016). This may have even occurred between ocean-foragers from Harrison

Cove and Moraine in 2019 as Harrison Cove birds made more dives at 40-90 metres depth than Moraine birds.

2.4.2 Differences in dive behaviour between colonies and years

Both inter-colony and inter-annual variation in dive behaviour was found for tawaki from Milford Sound. Significant effects of colony and year were detected for some dive parameters and often these effects were interactive with the directional effect and/or magnitude of variation between colonies dependent on the year.

In 2019, birds from Harrison Cove were diving significantly deeper, for longer and with higher descent rates than birds from Moraine, while in 2020 birds from Moraine dived significantly deeper, longer and had faster descent speeds than birds from Harrison Cove. Changes in dive behaviour such as these are likely due to environmental factors affecting prey distributions and prey availability which consequently modifies the diving behaviour of marine predators like penguins (Kooyman et al. 1992). For example, gentoo penguins that mainly fed on pelagic crustaceans would exhibit shallow dives while gentoos feeding on benthic fish made deep dives (Croxall et al. 1988). Over both years Moraine birds were diving almost exclusively in the open sea environment outside the fiord while Harrison Cove birds foraged almost exclusively in the fiord in 2020 but foraged both outside the fiord and within the fiord in 2019. Moraine birds foraging in the same general environment, yet still significantly changing their dive behaviour across years, supports the possibility that marine prey availability altered over this time. This is further highlighted by how 2020 Moraine birds made noticeably more wiggles at depths of 80-100+ metres than 2019 Moraine birds, indicating heightened foraging activity in this part of the water column in 2020, potentially as a result of prey being distributed deeper in the water column.

The lowered 2019 foraging efficiencies by tawaki at Harrison Cove compared with 2020, may indicate that prey and/or environmental conditions in both the fiord and ocean were not optimal in 2019. The deeper diving by Harrison Cove birds in 2019 and how two of the four birds with accompanying GPS tracks, foraged in the open sea, also diverges from their behaviour in past years where Harrison Cove birds rarely left the fiord when foraging (Mattern & Ellenberg 2016, 2017, 2018). However, it is difficult to know the true extent of the differences in 2019 Harrison Cove foraging behaviour due to our low sample size. In 2018, guard-stage birds foraging in the fiord rarely dived deeper than 30m but two post-guard

Harrison Cove birds were recorded diving deeper and making multi-day foraging trips outside the fiord (Mattern & Ellenberg 2018). The birds that foraged outside the fiord in 2019 were in guard stage, but it is possible that they were close to post-guard and raising older chicks with demanding nutritional needs, leading parents to expand their foraging ranges.

Past research on tawaki has shown that altered conditions in different years can be reflected in differences in diet, particularly in 2015-2016 during the ENSO event where there was a shift in δ15N stable isotope values of tawaki feathers (White 2020). Studies on the diet of tawaki have suggested small or larval stage schooling fish, winter-spawning squid, and krill as main dietary components (van Heezik, 1989,1990; Poupart et al. 2019). Future research sampling prey within and outside Milford Sound and identifying which species are key players in the diets of tawaki will be crucial for developing a better understanding of their foraging ecology. This would be particularly useful for determining the proportion of prey items that are pelagic versus benthic and what environmental changes/reductions in prey availability tawaki might be most vulnerable to.

Tawaki appeared to optimise their foraging, as other penguins have done (Tremblay & Cherel 2000) by consistently changing their descent velocity according to the maximum dive depth, with increasing depth associated with an increased descent velocity (see Appexdix 2, Figure A2.1). This same modulation of dive depth with speed has been reported in other penguin species and marine mammals (Wilson et al. 1997; Otani et al. 1998; Cherel et al. 1999) as they regulate buoyancy to reach their target maximum depth. In 2020, Harrison Cove birds dived to each depth class at significantly lower descent speeds than Moraine birds. Interestingly, in 2019 when Harrison Cove birds were actually foraging deeper more often, they neglected to increase their descent velocities with increasing depth past the 40m mark, suggesting Harrison Cove birds were using a different foraging strategy to Moraine birds.

2.4.3 Dive depth and duration: implications & limiting factors

Diving to deeper depths was central to the foraging strategy of 2020 Moraine birds. Increases in the frequency distribution of dives at 50m of depth onwards for Moraine birds in 2020 suggests a higher foraging effort at these depths. It appears that the Moraine foraging in 2020 could almost be split between two approaches – diving shallowly in the upper 20m of the water column or diving deeper past the 50m mark. There have been cases in the past where penguins from colonies that struggled to provide for their chicks dived deeper and showed

higher diving effort than conspecifics with shallower diving (Chiadiara et al. 2007). During surveys of the breeding sites in 2020 we found no chick deaths due to starvation and both colonies had examples of nests raising two chicks well past the stage where one should have died, tawaki being obligate brood reducers (St Clair 1992).

Although it seems that Moraine birds would naturally be at a disadvantage by expending more energy through diving deeper and longer than Harrison Cove birds in 2020, their average foraging efficiencies levelled out to be relatively similar. It is notable though, that 2020 Harrison Cove birds showed remarkably equal foraging efficiencies and dive durations throughout each daylight hour, whereas the foraging efficiencies and dive durations of Moraine birds changed markedly throughout the day. This is likely a result of Harrison Cove birds travelling only a small distance before instantly beginning to forage within the fiord where they can reliably encounter prey whereas Moraine birds must first complete a number of travelling dives out of the fiord before reaching their foraging grounds. This is also supported by the average number of dives per hour for 2020 Harrison Cove birds remaining more consistent than for Moraine birds who tend to complete fewer and fewer dives from the morning to the late afternoon, as they have been expending more time and effort diving deeper.

Considering that roughly 90% of trips made by Harrison Cove birds in 2020 occurred entirely within the fiord and over 90% of trips made by Moraine birds in 2020 were in the open sea, it is likely that differing foraging conditions and prey sources are contributing to the differences in foraging efficiency throughout the day. It can be assumed that diving to deeper depths was favourable for encountering prey in the open sea in 2020 and thus Moraine birds employed a strategy involving deeper, longer dives and faster descent rates. In contrast, food was clearly plentiful in the upper 20m of the water column for Harrison Cove birds foraging in the fiord, as this was where 85% of their dives occurred. Furthermore, prey appears to have been relatively reliable throughout the day, hence the temporally consistent foraging efficiencies and dive depths demonstrated by Harrison Cove birds. It should also be noted that the foraging efficiency of Moraine birds on trips greater than 24 hours in 2020, was significantly higher than the foraging efficiency of Moraine birds making short trips (see Appendix 2, Figure A2.2). This could be attributed to birds spending more time at foraging grounds and less time on travelling over the longer foraging trips. Moraine birds may forage more profitably on longer trips in the open sea as they can cover more foraging ground. This may

also explain why Harrison Cove birds might switch to longer trips outside of the fiord during post-guard when their chick has greater nutritional demands (Mattern & Ellenberg 2018).

The deepest dive a Harrison Cove bird made in the fiord was to 82m, while outside the fiord a Harrison Cove bird dived to 113m. Typography is not a limiting factor preventing fiord-foraging birds from diving deeper as the deepest part of Milford Sound is 300m. It is more likely that light conditions in the fiord often control the depth to which tawaki can forage successfully. Since penguins are primarily visual foragers (Martin & Young 1984; Sivak et al.1987), they rely on light availability at the depths they forage within. This aligns with the daily diving rhythms of many penguin species (Wilson et al. 1993; Walker & Boersma 2003) whose dive activity mainly occurs during daylight hours. Tawaki from colonies in Milford Sound generally follow this trend too, with only a few shallow (likely travelling dives) taking place prior to sunrise or after sunset. The deeper dives that did occasionally occur in the fiord, past 50 metres in depth, were likely made for the purpose of predator evasion, as there would be very little light at these depths.

New Zealand fiords have a low underwater light environment due to a combination of topographic shading by steep fiord walls as well as the presence of a buoyant, tannin rich low salinity layer (LSL) that attenuates light (Grange et al. 1981; Grange & Singleton 1988; Gibbs 2001). Gibbs (2001) reported that in Doubtful Sound visible light was attenuated by ~90% in the top 4m and then attenuated by another 5-10% in the next 15m. These values can't quite be applied to Milford Sound though, as characteristics of the Milford LSL may vary, and Doubtful Sound has a larger constant influx of freshwater from Lake Manapouri. Despite this, it is fair to assume that visibility in the fiord will be considerably low past 20-30 metres depth, compared to visibility below this depth in the open sea. Thus, it is logical that the vast majority of maximum dive depths occurred in the 0-20m range from fiord-foraging Harrison Cove birds. It further follows that when collating all 2019 and 2020 dives from Harrison Cove birds that were of known origin from GPS data (in versus out of the fiord), very few dives within the fiord reached deeper than 60 metres.

2.4.4 Behavioural flexibility in tawaki

It is clear not only from the considerable variation in dive behaviour between years and between colonies but also from the significantly low repeatability of dive behaviours within and among individuals, that tawaki foraging behaviour is flexible. Dives per hour, maximum

dive depth, dive duration and descent velocity all showed significantly low consistency both at the intra-individual and inter-individual level. Tawaki appear to adapt their behaviours to suit whatever foraging environment they may be in, on both a year-to-year, in-versus-out of the fiord and even on a trip-to-trip basis. A similar study on little penguins also reported high plasticity in individuals with low-moderate consistency in foraging parameters (Camprasse et al. 2017b). Intra-individual consistency appeared to be slightly higher for the parameters of maximum dive depth and descent velocity, indicating that these variables may be the most important features in an individual's diving strategy. Since the results presented here for tawaki represent only short term consistency during the chick guard stage, it would be worthwhile for future research to track their repeatability in other breeding stages such as incubation and post-guard, especially since recent research on African penguins has found that in difficult foraging conditions, consistency can be beneficial with individuals showing consistency in parameters such as dive duration demonstrating higher reproductive success (Traisnel & Pichegru 2019).

Preliminary differences observed in foraging and dive parameters gathered from Milford Sound tawaki, as compared to tawaki from Open Bay Island, also emphasise the suite of dive and foraging behaviours that tawaki can call upon depending on their location. At Open Bay Island, birds tended to dive shallowly when within the vicinity of the colony but made deeper dives further offshore (Poupart et al. 2019). A similar pattern can be seen in Moraine birds although they generally ranged further offshore and made longer trips both spatially and temporally than birds from Open Bay Island. However, it is hard to draw direct conclusions on the relative scarcity or richness of the foraging environments surrounding these locales since foraging data were collected in different years (primarily 2017 for Open Bay Island birds, compared to 2019-2020 for Milford Sound birds). Despite this, it does seem like Harrison Cove birds foraging in the fiord use a different strategy than the more typical oceanic foragers from Moraine and Open Bay Island, as evidenced by the heightened number of dives per hour seen in Harrison Cove birds. A strategy of diving more shallowly but more often per hour appears to allow Harrison Cove birds to effectively exploit prey items available in the fiord. The faster ascent and descent speeds observed in Milford Sound birds compared to Open Bay Island birds might also be part of a strategy to maximise time spent feeding/searching for prey in the bottom phase of their dives (Houston & Carbone 1992).

2.4.5 Limitations

Key limitations of this study include the small sample sizes of tawaki obtained, particularly from Harrison Cove in the year 2019, as well as the issues with acquiring GPS fixes within the fiord. Obtaining a small sample size is often the consequence of working with wild animals in logistically challenging locations but despite this, clear, differential patterns are still present between colonies and between years when looking at the combined picture of both the GPS tracks and dive behaviour. The relative consistency of results from Harrison Cove tawaki during the past years of 2015-2018 (Mattern & Ellenberg 2015; 2016; 2017; 2018) and 2020, where they primarily foraged in the fiord and made shallower dives than in 2019, corroborate the idea that 2019 was an unusual year for Harrison Cove tawaki. In future, it will be interesting to build a substantial dataset of repeat logger deployments on the same individuals to allow for more in-depth comparisons of environmental variability, when individual variability across years has been quantified.

Although the GPS tracks obtained from Harrison Cove birds were less cohesive than those from Moraine birds foraging in the ocean, this is unlikely to have confounded the data as the GPS tracks gathered still allowed the key analyses to depict the differential use of the fiord between Moraine and Harrison Cove birds. Furthermore, statistical measures such as subsampling were used to even out the GPS fixes across individuals and correct for differences in the numbers of GPS points sampled between years and colonies.

2.4.6 Conclusions

Tawaki from Milford Sound have shown differences in their foraging and diving behaviour based on their colony site and the environmental conditions they are subject to in different years. Tawaki from Harrison Cove and Moraine displayed contrasting dive behaviour across years, either adopting a strategy of deeper, longer dives with fast velocities or shallower, shorter dives with slower velocities. Foraging efficiencies for both colonies appeared to be greater in the year 2020 than 2019 although birds foraged differently to achieve this – Harrison Cove birds dived primarily to depths of 0-20m within the confines of the fiord while Moraine birds switched between shallower dives at this depth and longer dives in the deeper 60-120m of the water column of the open ocean. The clear segregation of foraging range areas in 2020 between Moraine and Harrison Cove birds, stresses the importance of not generalising the results from one colony to the wider population as even colonies situated

relatively close together can have considerable separation in their spatial use and diving strategies.

It is also evident that the dive behaviour of tawaki was partly a result of their foraging environment – either within the fiord where Harrison Cove birds often foraged or outside the fiord where Moraine birds foraged almost exclusively. Dives deeper than 60m rarely occurred in the fiord and this may be due to decreased light availability at deeper depths, making it difficult for visual predators to search for prey. The fiord ecosystem undoubtedly contains key foraging habitat for Harrison Cove tawaki and allows them to dive shallowly, only 5km from their colony site and still obtain enough prey to provide for their chicks. More work is needed, particularly in New Zealand fiords, to understand the types of prey tawaki forage for in this ecosystem. The shelter the fiord receives from the more unpredictable conditions of the open sea as well as the high nutrient input from run off, likely contribute to the creation of a rich ecological community that differs from the marine life present outside the fiord (Rutger & Wing 2006; Prebble et al. 2018).

This research has demonstrated complexity and plasticity in the foraging behaviour of tawaki. Their ability to substantially alter their diving behaviour across years as well as their low short-term consistency in dive parameters, demonstrate the highly flexible nature of tawaki foraging. Behavioural plasticity may well be a fundamental quality of any organism that lives in a system as dynamic as the marine environment, where prey distributions over time and space may vary considerably (Tremblay & Cherel 2003). Determining the degree of plasticity in the foraging behaviours of marine predators such as tawaki is vital to our understanding of how individuals and populations will cope with environmental change in the future.

Chapter 3: Environmental factors influencing the dive behaviour of fiord-foraging and ocean-foraging tawaki from Milford Sound

3.1 Introduction

Although the ocean may seem like a vast, homogenous space to the human eye, the marine landscape has a suite of environmental conditions that affect the distribution of marine life (Lescroël & Bost 2005). Oceanographic features including, currents, fronts and upwelling cells are often responsible for the concentration of biological resources such as prey, which in turn attract larger marine consumers (Pakhomov et al. 1994; Pollard et al. 2002; Bost et al. 2009). Apex predators are able to detect and follow physical processes, such as eddies and upwellings, allowing them to target the associated aggregations of predictable prey (Cotté et al. 2007; Dragon et al. 2010). Nevertheless, the location of prey can be impacted by oceanographic variation, resulting in alterations to prey availability in space and time on an annual or seasonal level (Xavier et al. 2013). Consequently, the foraging success of marine predators may be affected (Inchausti et al. 2003) and consumers may need to adapt their at sea movements or foraging behaviours to increase the likelihood of encountering prey (Weimerskirch 2007; Castillo-Guerrero et al. 2016).

In the oceanic sphere, cyclical changes can also result in variable environmental conditions leading to changes in marine productivity and the distribution of resources (Baduini 2003; Hoskins et al. 2008). One such cyclical pattern is the El Niño-Southern Oscillation (ENSO), an ocean-atmosphere fluctuation that occurs across the Pacific Ocean, altering the climate of the tropics and subtropics. The frequency and severity of El Niño events appear to be increasing due to anthropogenically induced climate change (Cai et al. 2014). Furthermore, more frequent El Niño events will likely dramatically modify oceanic food webs and cause shifts to the distributions of marine organisms, leading to decreased ocean productivity (Hoegh-Guldberg & Bruno 2010; DiLorenzo & Miller 2017). With lowered productivity and prey abundance, seabirds may be required to use more energy, change foraging strategies or switch prey species to enhance their foraging efforts (Harding et al. 2007; Ancona et al. 2012). Seabird species vary in their response to climatic events like El Niño, depending on their level of behavioural plasticity (Gilmour et al. 2018). Species that are highly adaptive or

plastic often continue to breed and successfully forage during El Niño events while species with less behavioural plasticity may fail to breed or experience significant population crashes (Duffy 1990; DiLorenzo & Miller 2017; Wingfeld et al. 2017).

Tawaki foraging off the west coast of New Zealand's South Island during the 2015 El Niño event experienced low foraging success, resulting in an abysmal breeding season (Mattern & Ellenberg 2015). El Niño events in New Zealand tends to result in stronger or more frequent westerly or south-westerly winds which can encourage dryness in eastern areas and more rain in the west (NIWA). Sea temperatures in the far western Pacific during El Niño usually cool below average. Tawaki from the Harrison Cove colony tracked in 2015, however, foraged solely within Milford Sound fiord, making remarkably shallow dives and having a very successful breeding season (Mattern & Ellenberg 2015). Including the current study, tawaki from Harrison Cove have been tracked over six years, through a range of different ENSO phases/strengths. Thus, comparing the dive behaviour of tawaki across these years in relation to the concurrent ENSO phase would provide insight into whether this climatic pattern is contributing to the foraging decisions of fiord based tawaki who can either forage within the fiord or the ocean outside.

Although the type and strength of ENSO event occurring during the tawaki breeding season may shed light on any large-scale controls on tawaki dive/foraging behaviour, it is necessary to investigate specific environmental factors to understand the dive behaviour of tawaki at a finer scale. Discovering what local conditions influence the foraging behaviour of tawaki is vital in predicting their degree of flexibility and potential responses to future environmental variability. When tawaki were tracked throughout their dispersal over the pre-moult period, environmental data from satellites were used along with K-select analysis to determine the importance of different oceanographic variables in the habitat selection of tawaki at their two possible journey destinations (Mattern et al. 2018). The environmental factors of water depth, surface current velocity and sea level anomalies had the greatest effect on the movements of birds headed to the Subantarctic Front (Mattern et al. 2018). In contrast, sea surface temperature (SST) and chlorophyll-a concentration were salient features for tawaki heading towards the Subtropical Front (Mattern et al. 2018). It is important to note, however, that while these oceanographic variables are informative for long range trips on a large spatial scale, they are not always relevant when investigating local scale foraging behaviour occurring over 1-50km.

No studies have hitherto compared the dive behaviour of tawaki directly to the environmental conditions that the birds experienced. Only one study to date (Poupart et al. 2019) has tracked tawaki and compared their finer scale foraging behaviour during the breeding season with environmental covariates. Even in this study, though, oceanographic variables were compared to the amount of time a birds spent foraging in areas with particular environmental features rather than aligning these features directly with dive behaviour. Thus, there is a gap in our understanding of how environmental conditions can explicitly influence dive behaviour in tawaki. There is some evidence from past research that physical features of the marine environment, such as salinity and sea surface temperature can impact diving patterns in seabirds (Lescroël & Bost 2005; Ramírez et al. 2014; Sutton et al. 2020). When tawaki from Open Bay Island were tracked, it was discovered that individuals mainly foraged along the continental shelf slope and their time spent foraging in one area was significantly influenced only by the surface salinity and bathymetry slope (Poupart et al. 2019). Hence salinity and seafloor bathymetry were also included in the analysis for Milford Sound tawaki to determine whether these variables remain equally important in governing the dive behaviour of fiord-foraging individuals in a different geographic locale.

Daily sea surface temperature was also chosen for analysis as an environmental feature since the summer breeding cousins of tawaki, the rockhopper and macaroni penguins have reportedly used temperature as a cue to locate optimum foraging conditions in the open ocean (Bon et al. 2015; Whitehead et al. 2016). Furthermore, other species such as king penguins preferentially forage in mesoscale frontal zones defined by SST gradients (Cotté et al. 2007). Chlorophyll-a concentrations and mixed layer thickness were two further variables included as environmental factors in the current study, due to previous research finding links between these variables and penguin foraging (Charrassin et al. 2002; Boersma et al. 2009). Prey may be more concentrated in the cold surface mixed layer while chlorophyll-a is an indicator of ocean productivity with prey often aggregating in areas of high chlorophyll (Charrassin et al. 2002; Boersma et al. 2009). There were no significant correlations of mixed layer thickness or temperature data to the foraging movements of tawaki from Open Bay Island, however it is unknown whether this is true across the full species range (Poupart et al. 2019).

For tawaki that foraged solely within the fiord (i.e. all bar one of the Harrison Cove birds tracked in 2020), oceanographic conditions could not be used to investigate local fiord-based diving behaviour. Thus, potentially influential environmental features unique to fiord-based

ecosystems were chosen. Fiords usually exhibit strong stratification with distinct water masses and a low salinity surface layer (LSL), formed due to rainfall and local freshwater supply (Rutger & Wing 2006). The surface layer can range between 2-10 metres in depth with a layer of warmer, undiluted seawater beneath (Stanton & Pickard 1981). Salinity and temperature at varying depths of the fiord water column, are environmental factors that can act as a proxy for the thickness of the LSL. Variation in the depth of this layer, as a function of freshwater input, may subsequently alter species composition within the fiord water column. In turn, the altered prey distribution may influence the foraging behaviour and dive depth of tawaki searching for marine pelagic species that inhabit the fiord.

The amount of rainfall in Milford Sound directly changes the thickness of the LSL and therefore, may be a principal variable regulating the dive behaviour of tawaki. Local wind is also a key environmental factor as it forces surface currents and circulation inside a fiord (Buckley & Pond 1976). The speed, and therefore strength of the winds within the fiord can induce horizontal and vertical circulation, leading to stronger currents and mixing within the upper water layers (Tande 2001; Stigebrandt 2012). Richly mixed surface layers due to a greater magnitude of wind may enhance prey circulation and result in favourable foraging conditions for tawaki, promoting them to forage within the fiord. Thus, wind speed may be an important environmental attribute in determining the dive behaviour of tawaki.

The current study aims to investigate how environmental variables varied over the 2019 and 2020 breeding seasons and determine which environmental factors influenced individuals foraging in both the fiord and the coastal ocean outside of Milford Sound. To test this, the study will compare key components of the dive behaviour of tawaki that foraged in the ocean with a suite of oceanographic variables. Key dive parameters of tawaki that foraged in the fiord will also be compared with a unique set of fiord-based environmental variables. To ascertain the presence of any large-scale patterns of dive behaviour in relation to ENSO activity, the strength and phase of the ENSO event occurring in each year will be compared across six years' worth of dive data from Harrison Cove tawaki. As past studies on marine predators have indicated, the dive behaviour of tawaki will likely alter as a result of being exposed to different environmental conditions while foraging. This study was established with the following predictions:

1. As was observed with the dive behaviour of Harrison Cove birds during the El Niño in 2015, it is expected that tawaki foraging under El Niño conditions dive more shallowly, with slower descent velocities and higher foraging efficiencies compared to birds foraging during La Niña conditions.
2. The fiord-based environmental conditions such as wind speed, rainfall, temperature and salinity will show significant changes across 2019 and 2020, reflecting the different foraging behaviours shown by the Harrison Cove colony across years (see Chapter 2).
3. The oceanographic conditions that tawaki foraged over such as SST, salinity, mixed layer thickness, chlorophyll-a and seafloor bathymetry will be significantly different across 2019 and 2020, reflecting the contrasting dive behaviour adopted by tawaki form the Moraine colony across years (see Chapter 2).
4. The dive behaviour (dive depth, descent velocity, foraging efficiency and number of wiggles) of fiord-foraging birds will be modified based on local environmental conditions such as salinity, temperature, wind speed and rainfall. Specifically, birds are expected to dive more shallowly and with slower descent velocities and higher foraging efficiencies at low salinities and low rainfall (i.e. a thin LSL) as visibility would be clearer and marine prey would be located higher in the water column.
5. The dive behaviour (dive depth, descent velocity, foraging efficiency and number of wiggles) of ocean-foraging birds will be impacted by oceanographic conditions such as SST, salinity, mixed layer thickness, chlorophyll-a, and seafloor bathymetry. Specifically, birds are expected to alter their dive behaviour over areas of cooler SST and higher chlorophyll-a concentrations as prey are more likely to aggregate under these conditions.

3.2 Methods

3.2.1 Study area

Tawaki were sampled from two colonies breeding within Milford Sound, Fiordland (44.6414° S, 167.8974° E), a fiord on the southwest of New Zealand's South Island. The fiord sits within Fiordland National Park and the northern side of Milford Sound is protected by the Piopiotahi Marine Reserve. The Harrison Cove colony (-44.624°, 167.913°) lies near the

mouth of the Harrison River while the Moraine colony (-44.604°, 167.809°) is situated on the southern side of the fiord, opposite Dale Point.

3.2.2 Deployment and retrieval of data loggers

Research took place over two consecutive breeding seasons in 2019 and 2020. GPS dive loggers were deployed on adult females when penguin pairs were in the chick guard stage of breeding. The 2019 field season began late, on the 27th of September and continued until the 19th of October while the 2020 field season began on the 8th of September and continued through to the 15th of October.

On their return from foraging, and after allowing them time to feed their chicks and rest, adult females were captured at the nest by hand or with the aid of a leg crook for the more inaccessible nests. Once captured, birds were fitted with a cloth hood to minimise stress and weighed using a 5kg spring scale (±10g; Pesola). To quantify their foraging movements, habitat use, and diving behaviour, birds were equipped with a combination GPS dive logger (Axy-Trek Marine, Technosmart) recording location, depth (±10 mbar of pressure), and temperature (± 0.2°C) every 1 s and tri-axial body acceleration at 25 Hz (40 x 20 x 8 mm, 14g). In 2019, the loggers were programmed to take 1 fix per minute, excepting throughout the non-peak foraging period of 2300-0400 h, when they were programmed to take 1 fix every 15 minutes. In 2020, a different programming regime was used to attempt to extend the devices' battery life and to gain data on multiple foraging trips. The 2020 loggers' sampling regime was thus set to record, in theory, a GPS position every 3 minutes or every second dive (an average tawaki dive lasts 1.5 minutes). Similar to the 2019 regime, between the non-peak foraging period of 2300-0600 h, the devices were programmed to take a fix only every 15 minutes.

The devices were attached to the midline dorsal feathers on the lower back with waterproof tape (TESA 4651; Beiersdorf AG) following Wilson et al. (1997). In total, attached devices represent well under 1% of the penguins' body mass in air and are therefore likely to have negligible impact on the individual's foraging behaviour (Agnew et al. 2013). Handling procedures lasted ~10 minutes before birds were released near their nest to resume normal behaviours. After 4-5 days of wearing the device (their projected maximum battery life), individuals were recaptured, and the data loggers removed. Devices were recovered by either

recapturing logger-equipped penguins shortly after their landing on an access track to their colony site or by recapturing them at the nest if they were initially missed at the landing.

3.2.3 Data analysis

Harrison Cove dive behaviour from 2015-2020 in relation to ENSO activity

Dive data collected by The Tawaki Project (Mattern & Ellenberg 2015; 2016; 2017; 2018) from past breeding seasons (2015-2018) was obtained in order to compare the key dive parameters across five years and discern how unique the behaviour of 2019 Harrison Cove birds was in a more detailed context. The four key dive parameters of descent velocity, dive depth, foraging efficiency and number of wiggles were chosen for comparison as they each represent a key component of dive behaviour. Furthermore, dive depth, descent velocity and foraging efficiency were all found to vary significantly between 2019 and 2020 (see Chapter 2). Dive duration was not included since it is so highly correlated with dive depth, as is ascent velocity with descent velocity. Descent velocity is correlated with dive depth but not to the same degree as dive duration, and the nature of this relationship did change over the years and between colonies (see Appendix 2, Figure A2.1).

The Oceanic Niño Index (ONI) provides a measure of the type of ENSO event occurring throughout the months of the year. ONI was sourced (Climate Prediction Center - ONI (noaa.gov)) and averaged between the two breeding months when tawaki were tracked during guard stage (September and October). The ONI of each year was compared against the average dive depth, descent velocity, number of wiggles and foraging efficiency of tawaki tracked from Harrison Cove during those years, to determine whether any larger-scale trends were present in the birds' dive behaviour in relation to the type and/or strength of the concurrent phase of the El Niño Southern Oscillation (ENSO).

Comparison of environmental factors within the fiord in 2019 and 2020

From the period of 1 September – 15 October in both 2019 and 2020, daily environmental data were sourced from a local weather station or monitoring buoy and averaged to allow comparison across the years. The time period chosen represents a core period of the tawaki breeding season and encompasses the days in which tawaki were actively tracked over both

years. Daily measurements of total rainfall and average wind speed were collated from the Milford Sound Electronic Weather Station on NIWA's Clifllo database (https://cliflo.niwa.co.nz). Daily measurements of the temperature and salinity at 0.5m, 1.0 m, 1.5 m, 2.0 m, 3.0 m, 5.0 m, 7.0 m, 9.0 m, 11.0 m and 19.0m from sensors at an oceanographic mooring in the Milford Marina, were provided by Meridian Energy. The sensor data at depth 0.5m was chosen for use in analysis of temperature and salinity as this gives the most precise level of how thin/saline the low salinity layer (LSL) is and 0.5m was also the shallowest accepted dive from tawaki in dive data analyses.

Bar graphs were made using R (R Core Development Team 2021), to compare the means and standard errors of temperature, salinity, rainfall and wind speed over the given period. A Type II ANOVA test was performed on the data to determine whether the four environmental variables were significantly different across the years 2019 and 2020.

Impact of environmental factors on the dive behaviour of fiord-foraging birds

The dive dataset was split between birds who foraged in the fiord and birds who foraged in the ocean. Since only one bird with accurate dive data was known to forage solely within the fiord in 2019, only fiord-foraging birds from 2020 were used in the analysis of environmental variables on dive behaviour. The dataset was also filtered to only include dive events that had at least 3 wiggles occur (ensuring that the dives included were more likely to be true foraging dives). After initial testing using daily measurements of environmental data in Milford Sound, data was obtained at hourly intervals instead, to increase the temporal resolution and accuracy of results (see Appendix 3, Table A3.1). Hourly environmental data on the wind speed, salinity and temperature was then matched with the same hour of the dive events for each bird. Each dive event was also aligned with the total rainfall of the hour before the dive event occurred, as this variable acts as a proxy for the amount of rainfall a bird has most recently experienced. Conversely, the measurement of salinity from the oceanographic monitoring buoy provides insight into the larger scale or accumulative degree of freshwater input to the fiord.

Statistical analyses were completed in R and linear mixed models (LMMs) were made to investigate the effect of the environmental variables on the dive parameters of descent velocity, dive depth and foraging efficiency. A generalised linear mixed model (GLMM) with

a negative binomial family and Poisson link function was used for the dive parameter of number of wiggles. Temperature and salinity measurements from the oceanographic mooring were found to be highly correlated as shown by correlation plots and a high variance inflation factor when they were included together in a model. Consequently, temperature was removed from the models. Prior to inclusion in the models, all environmental variables were scaled using the package 'arm.' Two birds in the dataset went on 3-4 trips but in order to resolve convergence issues, only trips one and two were included in the dataset for the response variables of dive depth, descent velocity and number of wiggles with the random effects structure of trip identity nested within bird identity. Dive depth was square root transformed for normality before being included in the model. For the linear mixed model with foraging efficiency as the response variable, only trip one was included to decrease the complexity of the model and allow convergence, with the random effect as bird identity. All three LMMs tested for the full main and interactive effects of rainfall, salinity and wind speed. The GLMM tested for the effects of salinity and rainfall as otherwise the model became too complex to run and these two variables appeared to carry the most impact in the other models.

For all four models, the residuals were plotted and visually checked to ensure there were no signs of abnormal patterns or heteroscedasticity. Due to the presence of significant interactions, type III analysis of variance tables with Satterthwaite's method were produced to assess the significance of the fixed effects and their interactions, using packages 'lmtest' and 'lme4.' For the GLMM on number of wiggles, a type II Wald chi square test was performed to assess the significance of the main effects of salinity and rainfall. Using the function 'r.squaredGLMM' from the package 'MuMIn' the conditional and marginal coefficient of determination for all four mixed-effect models were computed. Conditional R^2 represents the variation in the dataset explained by the full model while the marginal R^2 represents the variation in the dataset solely attributable to the random effects included in the model.

Plots of model predictions for the fixed factors in the models were produced using the packages 'ggplot' and 'ggeffects.' To visually display model predictions of the interactive effects of between environmental variables, rainfall levels of 0mm, 4mm and 10mm were chosen to represent no rain, moderate rain and heavy rain, respectively.

Comparison of environmental factors encountered by ocean-foraging birds in 2019 and 2020

Environmental factors were gathered from satellite data to be matched with tawaki GPS tracks and dive events (see Appendix 3, Table A3.1). Seafloor bathymetry was sourced from NIWA's 2016 250m gridded bathymetry dataset (www.niwa.co.nz/our-science/oceans/bathymetry). The daily sea surface temperature (SST) was gathered at 0.01° resolution (https://coastwatch.pfeg.noaa.gov/) while daily mixed layer thickness and salinity were obtained at 0.08° resolution and chlorophyll-a at 0.25° resolution (http://marine.copernicus.eu/). Raster layers of these variables were projected on to ArcMap and aligned with the GPS points of ocean-foraging birds over 2019 and 2020. Each GPS point had accompanying dive data. Spatial joins were made to extract the grided environmental data to the bird's GPS/dive data before the correct dates were manually checked and assigned in excel. The resulting dataset of environmental conditions encountered by the birds while foraging was used to create bar graphs comparing the means and standard errors of SST, salinity, seafloor bathymetry, mixed layer thickness and chlorophyll-a between the years 2019 and 2020. To develop an idea of how the 2019 and 2020 ocean foraging environments differed, LMMs were used with each environmental variable as the response and year as the fixed factor, including a random effects structure of trip identity nested within bird identity, Type II Wald chi square tests were used to determine whether the five environmental variables were significantly different across 2019 and 2020. For all five models, the residuals were plotted and visually checked to ensure there were no signs of abnormal patterns or heteroscedasticity.

Impact of environmental factors on the dive behaviour of ocean-foraging birds

Utilising the oceanographic data that was previously spatially matched to the birds' dive events, models were produced to determine the effects of key environmental variables (chlorophyll-a, SST, seafloor bathymetry, MLT, salinity) on four dive parameters – descent velocity, dive depth, foraging efficiency and number of wiggles. The variable of year (2019/2020) was also included in the models since sufficient ocean-foraging data was collected across years. Only one trip per bird was included in the dataset to decrease the complexity of the random effects structure in the models. The dataset was also filtered to only include dive events that had at least 3 wiggles occur (ensuring that the dives included were more likely to be true foraging dives).

Initially, all environmental variables of SST, salinity, mixed layer thickness, seafloor bathymetry and chlorophyll-a were included in LMMs for dive depth, descent velocity and foraging efficiency and a GLMM for number of wiggles. Akaike Information Criteria (AIC) was used with multi-model inference to determine the best set of environmental predictor variables to include in the models for descent velocity, dive depth, number of wiggles and foraging efficiency (see Appendix 3, Table A3.2). Prior to analysis all environmental variables were standardised using the package 'arm.' Model selection was performed on R using the 'dredge' function with rank set as "AICc" and the packages 'MuMIn' and 'MASS' downloaded. The relative importance (the sum of the Akaike weights of the models in which the variable was present) of each variable was calculated. A variable that is in all the well-supported models has an importance close to 1.0. This enabled a comparison of the environmental variables used, as a variable included in only one well-supported model is considered less influential on tawaki dive behaviour than a variable included in the majority of closely ranked models.

Since solely choosing variables for a final model based only on their relative importance has been contested in the past (Galipaud et al. 2017), AIC model averaging was also completed. The model-averaged coefficients and confidence intervals were computed for each environmental variable, and for each dive parameter although the variable of year (2019/2020) was not included in the model selection for number of wiggles as this made model convergence difficult. Environmental variables were included in the final model if they had a high variable importance (>0.95) and/or non-overlapping 95% confidence intervals (see Appendix 3, Table A3.2).

The final environmental models with were re-run as LMMs with the random effect of bird identity to investigate the effect of influential environmental variables on the dive parameters of descent velocity, dive depth and foraging efficiency. A GLMM with a negative binomial family and Poisson link function was used for the dive parameter of number of wiggles, with bird identity as a random effect.

Variance inflation factors (VIF) were checked to determine if any co-linearity was present in the models. For the dive depth and descent velocity models, there was slight co-linearity between seafloor bathymetry and salinity, however VIF's were all still below 3 so the models were not altered. To enhance interpretability of the results, interactive effects were not included in the models. Dive depth was square root transformed for normality and descent

velocity was log10 transformed before being included in the models. Plots of model predictions for the fixed factors in each model were produced using the packages ‘ggplot’ and ‘ggeffects.’ Using the function ‘r.squaredGLMM’ from the package ‘MuMIn’ the conditional and marginal coefficient of determination for all four mixed-effect models were computed.

For all four models, the residuals were plotted and visually checked to ensure there were no signs of abnormal patterns or heteroscedasticity. Type II Wald chi square tests were performed to assess the significance of the fixed effects, using packages ‘lmtest’ and ‘lme4.’

3.3 Results

3.3.1 Dive behaviour of Harrison Cove birds in relation to ENSO activity

On average, tawaki tracked from the Harrison Cove colony in 2019 dived deeper and with faster descent velocities than tawaki in any other year between 2015 and 2020 (Table 3.1). The ONI in 2019 was reported as ‘normal’ meaning that there was no departure from normal sea surface temperatures during the breeding season. In 2016, tawaki also dived noticeably deeper and with faster descent velocities than in other years, although in this year the ONI was indicative of a weak La Niña, where sea surface temperatures are warmer (Table 3.1). Despite both 2016 and 2017 sharing a weak La Niña with the exact same ONI, the dive parameters of tawaki were very different (Table 3.1). Tawaki tracked in 2017 had very shallow dive depths and slow descent velocities, more akin to the maximum dive depths and descent velocities reported in the strong El Niño year of 2015 (Table 3.1).

Foraging efficiencies also differed between 2016 and 2017 with the lowest foraging efficiencies of all the years occurring in 2017 (Table 3.1). Apart from 2017 and 2020, foraging efficiencies were generally similar across the years, regardless of the differing ONI (Table 3.1). In 2020, the average foraging efficiency was the highest at 0.42 and this occurred during a moderate La Niña (Table 3.1). Number of wiggles per dive was variable across the years although the highest number of wiggles occurred during the moderate La Niña of 2020, closely followed by the year of normal weather conditions in 2019. The weak La Niña in 2016 also had a slightly elevated number of wiggles compared to 2015, 2017 and 2018. Overall,

there were no decisive trends found between the strength and type of ONI in each year and the dive depths, descent velocities and foraging efficiencies of tawaki.

Table 3. 1 Summary of how the four key dive parameters of maximum dive depth, descent velocity, number of wiggles and foraging efficiency, of birds from Harrison Cove in Milford Sound, have changed over the years 2015-2020 and the corresponding Oceanic Niño Index (ONI) and type of El Niño Southern Oscillation phase occurring during the months of September-October when the birds were tracked. Values shown are means and standard deviations calculated across individuals (n: 2015 = 6; 2016 = 4; 2017 = 5; 2018 = 5; 2019 = 4; 2020 = 8).

Year	Maximum Dive Depth (m)	Descent Velocity (m/s)	Number of Wiggles	Foraging Efficiency	ONI	Type
2015	10.72 ± 9.08	0.73 ± 0.30	6.7 ± 4.8	0.38 ± 0.17	2.4	Very Strong El Niño
2016	19.47 ± 14.7	0.92 ± 0.39	7.8 ± 4.8	0.36 ± 0.16	-0.7	Weak La Niña
2017	10.67 ± 3.24	0.67 ± 0.35	6.2 ± 4.5	0.33 ± 0.26	-0.7	Weak La Niña
2018	14.04 ± 9.92	0.87 ± 0.31	6.3 ± 4.2	0.38 ± 0.17	0.8	Weak El Niño
2019	24.7 ± 20.6	0.94 ± 0.38	8.3 ± 5.9	0.38 ± 0.15	0.3	Normal
2020	16.3 ± 18.0	0.83 ± 0.32	8.9 ± 5.4	0.42 ± 0.17	-1.2	Moderate La Niña

3.3.2 Conditions in the fiord environment in 2019 and 2020

In 2020, the salinity at 0.5m depth ranged between 0.75 and 28 PSU, the temperature ranged between 6.8 and 12 °C, the hourly total rainfall ranged between 0mm and 15.8mm and the wind speed varied between 1 and 360 m/s. The mean daily rainfall in Milford Sound between the 1st of September to the 15th of October was much higher in 2020 compared to 2019 and this difference was statistically significant (ANOVA, F = 4.77, P = <0.05; Figure 3.1). Mean temperature and mean salinity in the fiord at 0.5 metres of depth were also significantly lower in 2020 compared to 2019 (ANOVA, F = 53.1, P = <0.001; ANOVA, F = 60.67, P = <0.001; Figure 3.1). Mean wind speed appeared to be slightly lower in 2019 than in 2020, however, this difference was not statistically significant (ANOVA, F = 2.80, P = 0.098; Figure 3.1).

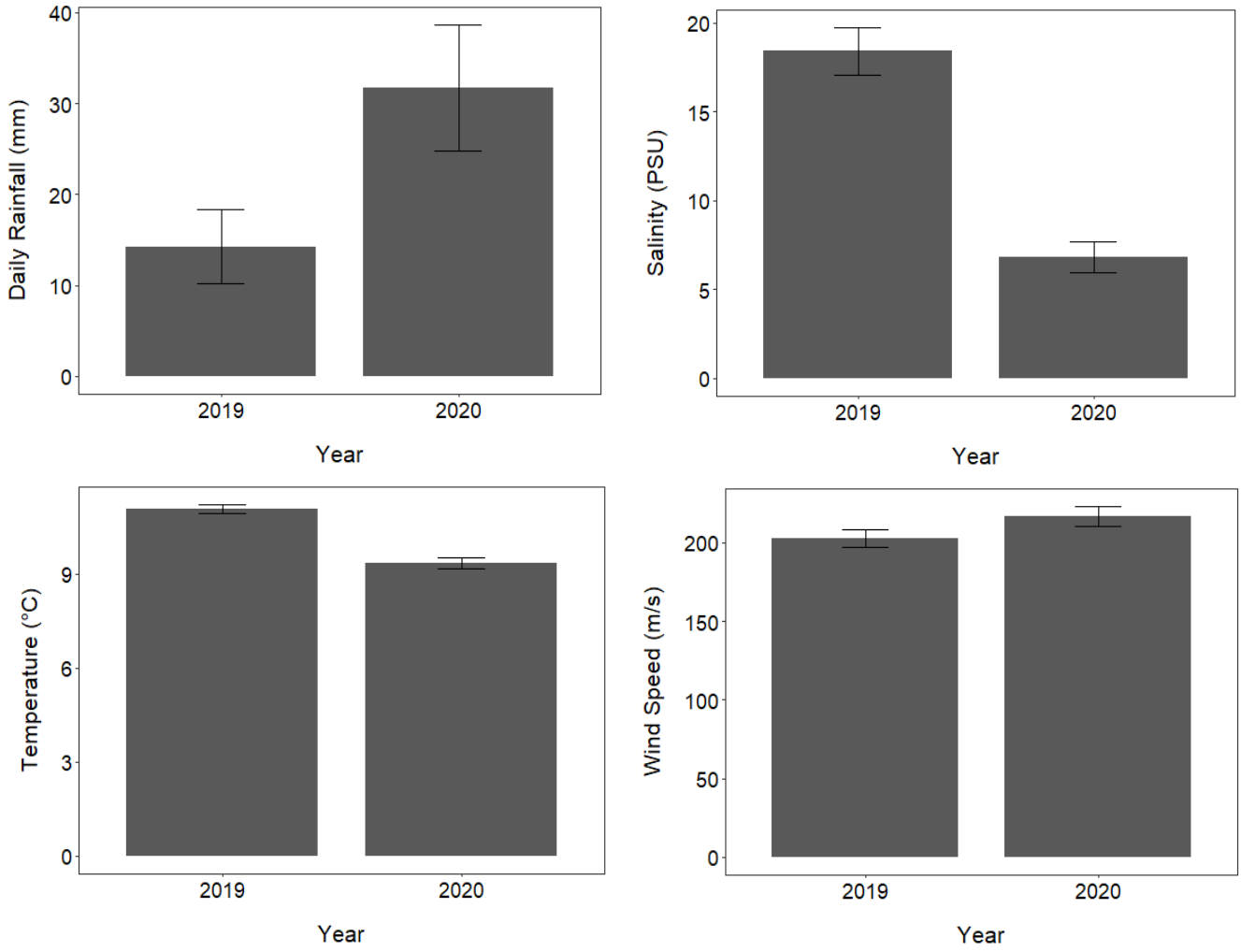

Figure 3.11 The mean (± standard error) of environmental conditions in Milford Sound fiord throughout the core breeding season (1s September – 15th October) between the years 2019 and 2020. Wind speed and daily rainfall were sourced from the Milford Sound weather station, temperature and salinity measurements were taken from a monitoring buoy situated in the inner fiord near Milford Marina at 0.5m depth.

3.3.3 Impact of environmental factors on the dive behaviour of fiord-foragers

The interaction between the environmental factors of salinity and rainfall and the interaction between rainfall and wind speed were found to significantly influence the dive parameters of maximum dive depth and descent velocity (Table 3.2). Models including salinity, rainfall, wind speed and their interactions were reported to explain 59% of the variation in maximum dive depth and 70% of the variation in descent velocity for fiord-foraging birds (Table 3.2). For maximum dive depth, 14% of this variation was attributable to the random effects of the

trip identity and bird identity (Table 3.2). For descent velocity, the random effects in the model were found to explain 17% of the variation in the descent velocity (Table 3.2).

The model predictions computed from the LMMs suggested that heavy rainfall of 10mm in the preceding hour, and low salinity in the fiord results in tawaki diving more shallowly and with slower descent velocities than when no rainfall has occurred in the previous hour (Figure 3.2; Figure 3.3). Comparatively, with heavy rainfall in the preceding hour, and high salinity in the fiord, tawaki were predicted to dive more deeply and descend more quickly compared to when no rainfall has occurred in the previous hour (Figure 3.2; Figure 3.3). With only a little amount of rainfall occurring in the previous hour, the dive depth of tawaki did not appear to alter with salinity, although descent velocity was predicted to be higher at low salinities (Figure 3.2; Figure 3.3). It was necessary to display the square root of the maximum dive depth rather than raw dive depth because the square root transformation greatly improved the normality of this dive parameter and altered the severity of the shape of the predicted interactions.

Visual plots of the model predictions are valuable for assessing trends as predicted by the model, however, they do not always make predictions within reasonable bounds of biology. It is important to note that the predictions for the 0mm of rainfall at high salinities predict descent velocities that have confidence intervals below 0 m/s. This does not make biological sense and is likely a result of not enough data points being obtained at higher salinities in the fiord, thus higher confidence intervals exist in the zone of salinities between 20-30 PSU.

At low wind speeds and 0mm of rainfall in the preceding hour, shallower dive depths and lower descent velocities were predicted as compared to dives occurring after recent heavy rainfall (Figure 3.2; Figure 3.3). In comparison, at higher wind speeds and 0mm of rainfall, deeper dive depths and faster descent velocities were predicted compared to dives taking place at higher wind speed and after heavy rainfall (Figure 3.2; Figure 3.3). However, the model predictions for dive depth and descent velocity do have interactions between wind speed and rainfall that have substantial overlapping confidence intervals (Figure 3.2; Figure 3.3). Thus, it may be possible that descent velocity and maximum dive depth do not truly alter depending on the interactive effects of wind speed and recent rainfall.

The model including salinity, rainfall, wind speed and their interactions as fixed effects was reported to explain 25% of the variation in foraging efficiency in tawaki with 10% of this variation being attributable to the random effect of bird identity (Table 3.2). However, effects of wind speed, rainfall, salinity and their interactions had no significant impact on the foraging efficiency of fiord-foraging birds (Table 3.2; Figure 3.4).

The model including salinity and rainfall as fixed effects was reported to explain 26% of the variation in foraging efficiency in tawaki with 7% of this variation being attributable to the random effects of trip identity and bird identity (Table 3.2). Salinity was found to significantly influence the number of wiggles in fiord-foraging tawaki (Table 3.2). Tawaki were predicted to have more wiggles in the dives made at lower salinities in Milford Sound while dives at higher salinities had less wiggles (Figure 3.5). However, there was still slight overlap between confidence intervals surrounding the predicted number of wiggles at either end of the scale of salinities (Figure 3.5).

Table 3. 2 Summary table displaying the model parameters and results for LMMs investigating the effects of environmental variables (hourly salinity at 0.5m, rainfall in the previous hour and hourly wind speed) and their interactions on the three dive parameters of maximum dive depth, descent velocity and foraging efficiency. A GLMM was used to test the effects of salinity and rainfall on number of wiggles. Test statistic was the F value for the LMMs and the X^2 value for the GLMM. Trip ID nested within bird ID were included as random effects in the models for maximum depth, descent velocity and number of wiggles while a reduced dataset with only one trip per bird was used for foraging efficiency, with bird ID as the random effect. P values in bold are under the set significance level of <0.05.

Response Variable	Explanatory Variables	Estimate	CI (lwr, upr)		Test Statistic	P value	Marginal R^2	Conditional R^2
Max dive depth (m)	Salinity	-0.38	-0.88	0.15	2.50	0.11	0.14	0.59
	Rainfall	-0.47	-1.06	0.21	2.51	0.11		
	Wind Speed	-0.34	-0.77	0.08	2.70	0.10		
	Salinity*Rainfall	1.95	0.60	3.22	8.97	**<0.01**		
	Salinity*Wind Speed	0.83	-0.06	1.72	3.47	0.06		
	Rainfall*Wind Speed	-1.74	-2.99	-0.55	8.74	**<0.01**		
	Salinity*Rainfall*Wind Speed	1.42	-1.02	3.89	1.30	0.25		
Descent velocity (ms^{-1})	Salinity	-0.29	-0.40	-0.18	30.3	**<0.001**	0.17	0.70
	Rainfall	-0.12	-0.25	0.03	3.61	0.06		
	Wind Speed	-0.09	-0.19	0.00	3.96	**<0.05**		
	Salinity*Rainfall	0.37	0.08	0.64	6.74	**<0.05**		
	Salinity*Wind Speed	0.16	-0.03	0.36	2.80	0.09		
	Rainfall*Wind Speed	-0.40	-0.67	-0.14	9.59	**<0.005**		
	Salinity*Rainfall*Wind Speed	0.37	-0.16	0.92	1.9	0.17		
Foraging Efficiency	Salinity	-0.04	-0.19	0.11	0.22	0.64	0.10	0.25
	Rainfall	-1.60	-0.59	0.27	0.48	0.49		
	Wind Speed	0.01	-0.19	0.22	0.01	0.92		
	Salinity*Rainfall	0.15	-0.42	0.79	0.24	0.63		
	Salinity*Wind Speed	0.22	-0.07	0.50	2.14	0.15		
	Rainfall*Wind Speed	0.15	-0.70	1.01	0.12	0.73		
	Salinity*Rainfall*Wind Speed	0.59	-0.57	1.79	0.91	0.34		
Number of Wiggles	Salinity	-0.02	-0.03	-0.01	14.0	**<0.001**	0.07	0.26
	Rainfall	-0.02	-0.04	0.01	1.58	0.21		

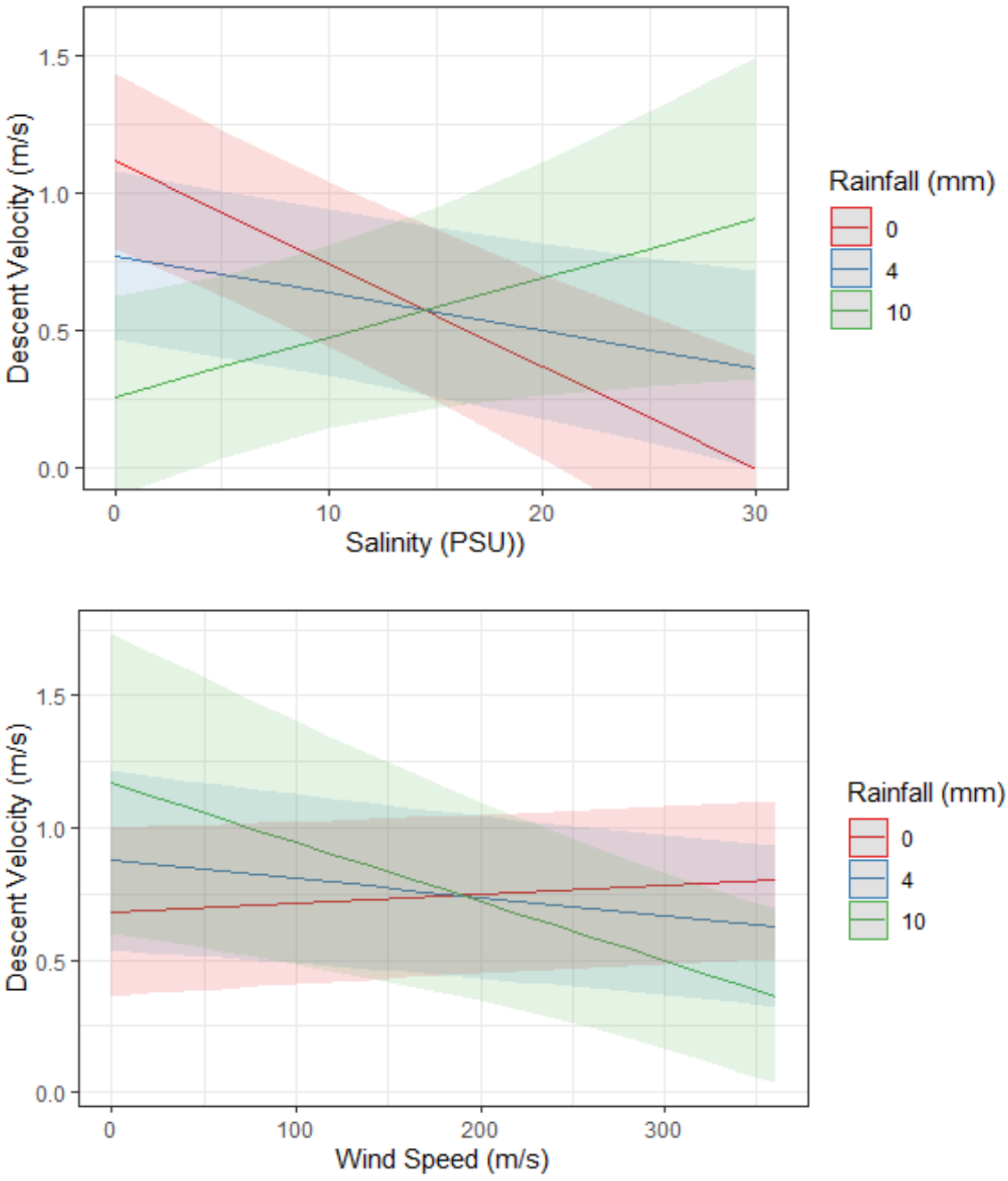

Figure 3.2 Plotted model predictions of the interactive effects of salinity (top) and wind speed (bottom) at varying levels of rainfall, on the descent velocity of tawaki foraging within Milford Sound (n = 8). Wind speed and salinity inputs were measured hourly while rainfall measurements were taken from the previous hour. Salinity was measured at 0.5m depth. Rainfall levels of 0,4 and 10mm represent no rain, moderate rain and heavy rain, respectively.

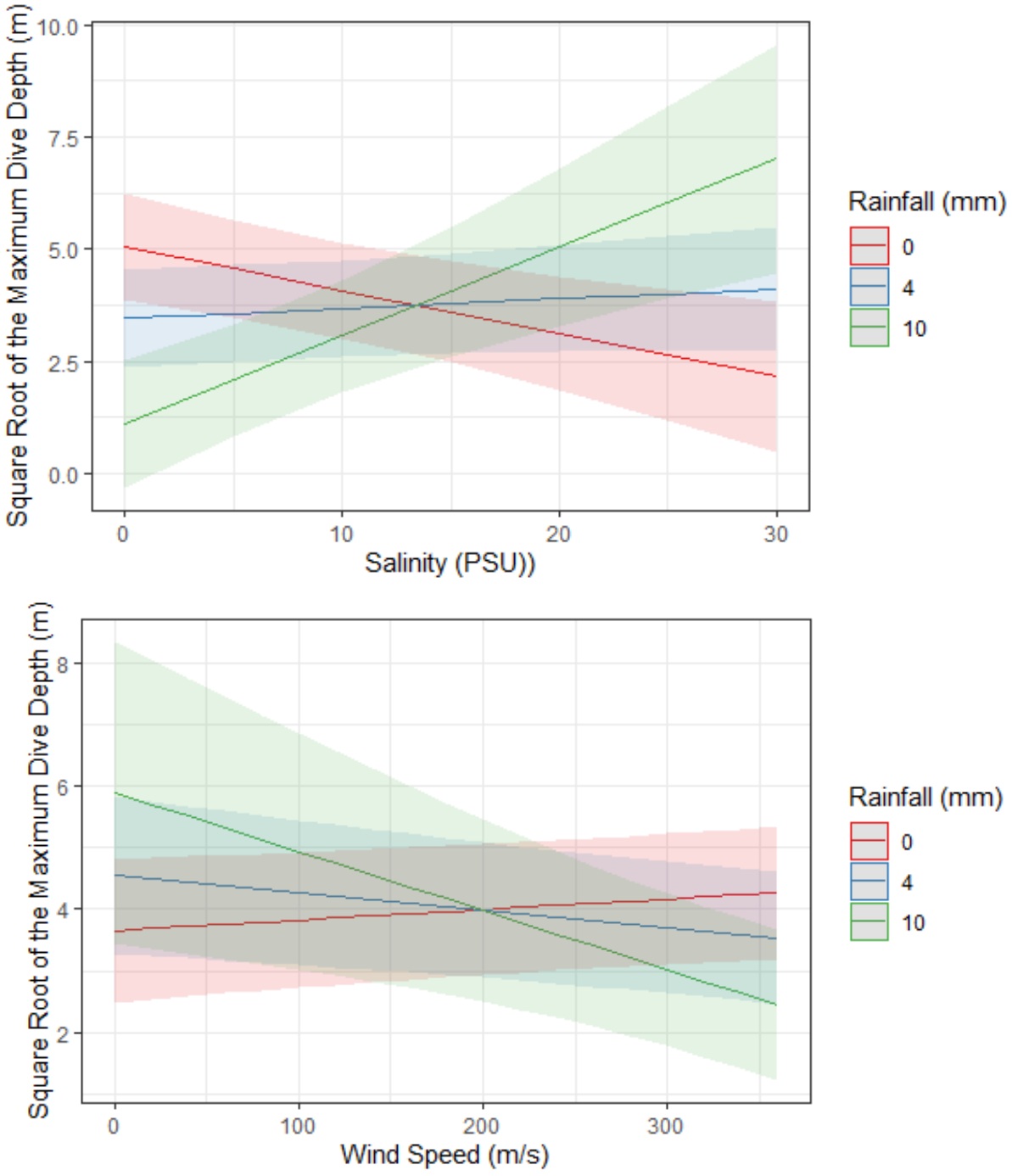

Figure 3.3 Plotted model predictions of the interactive effects of salinity (top) and wind speed (bottom) at varying levels of rainfall, on the maximum dive depth (square root transformed) of tawaki foraging within Milford Sound (n = 8). Wind speed and salinity inputs were measured hourly while rainfall measurements were taken from the previous hour. Salinity was measured at 0.5m depth. Rainfall levels of 0,4 and 10mm represent no rain, moderate rain and heavy rain, respectively.

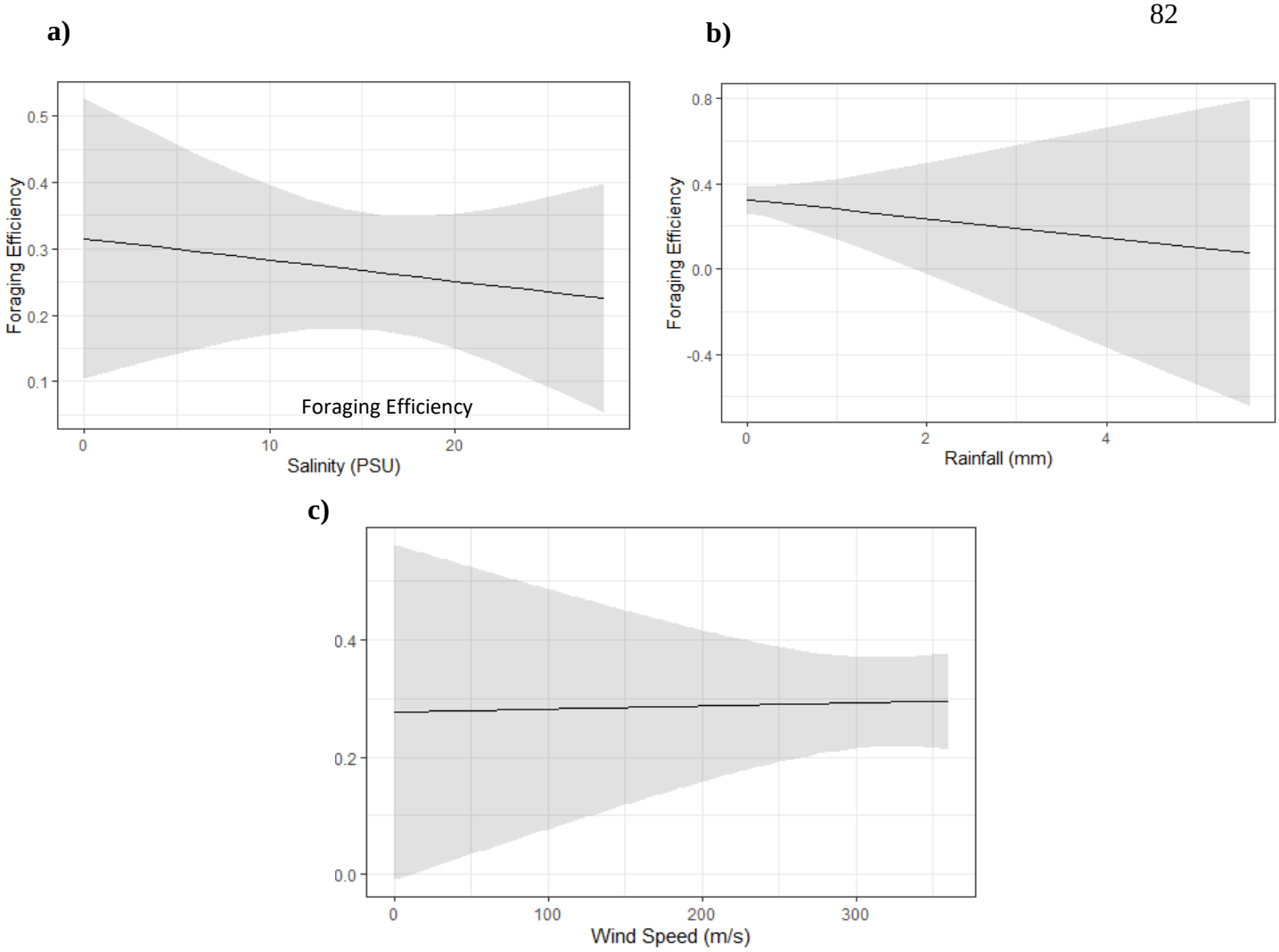

Figure 3.4 Plotted model predictions of **a)** salinity, **b)** rainfall and **c)** wind speed on the foraging efficiency of tawaki foraging within Milford Sound (n = 8). Wind speed and salinity inputs were measured hourly while rainfall measurements were taken from the previous hour. Salinity was measured at 0.5m depth.

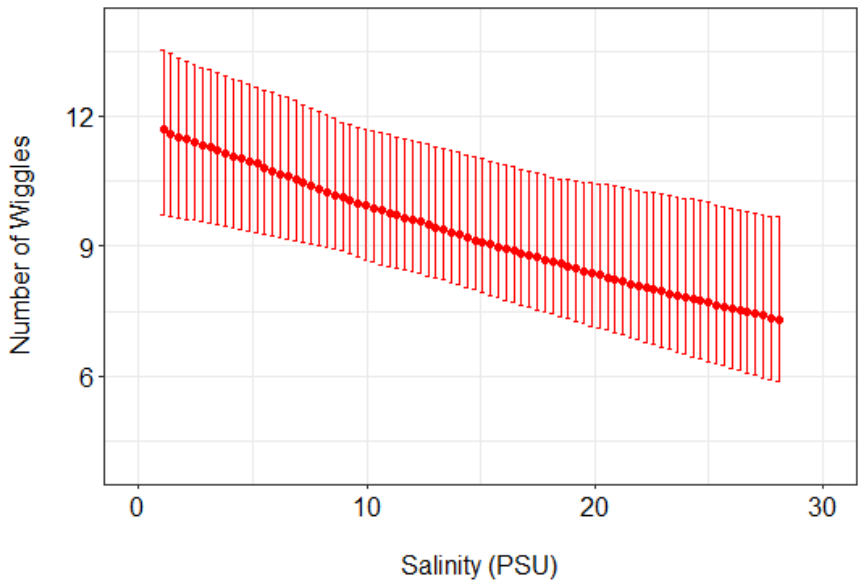

Figure 3.5 Plotted model predictions of the effect of salinity on the number of wiggles of tawaki foraging within Milford Sound (n = 8). Salinity was measured at 0.5m depth.

3.3.4 Conditions in the ocean environment in 2019 and 2020

When foraging outside Milford Sound in 2019, the dives of most tawaki took place in oceanic waters (>1000m, 42%) followed by neritic waters (0-200m, 37%) and shelf slope waters (200-1000m, 21%). In 2020, however, tawaki foraged primarily in neritic shelf waters (56%) and split the rest of their dives between oceanic (24%) and shelf-slope (20%) waters. In the waters tawaki foraged over in 2019, the SST varied between 11.5 and 12.5 °C, the salinity between 34.7 and 35.1 PSU, the mixed layer thickness between 10 and 105 m deep and the chlorophyll-a concentrations lay between 0.47 and 1.2 mg/m^3. In 2020, the SST ranged between 12 and 13.5 °C, salinity between 34.3 and 35.1 PSU, the mixed layer thickness between 10 to 26 m deep, and the chlorophyll-a concentrations varied between 0.35 and 0.91 mg/m^3.

The mean SST encountered by tawaki while foraging in the ocean outside Milford Sound was higher in 2020 compared to 2019 and this difference was statistically significant (LMM, X^2 = 3210, P = <0.001; Figure 3.1). The salinity of the ocean over which birds foraged was very slightly lower for birds foraging in 2020 than in 2019 (LMM, X^2 = 30.82, P = <0.001; Figure 3.1) Mean mixed layer thickness was significantly deeper in 2019 as compared to 2020 (LMM, X^2 = 92.61, P = <0.001) while mean chlorophyll-a concentration was higher in 2020 than 2019 (LMM, X^2 = 8395, P = <0.001; Figure 3.1). It also appeared that tawaki foraged over waters that were of shallower seafloor bathymetry in 2019 than in 2020 (LMM, X^2 = 5227, P = <0.001; Figure 3.1).

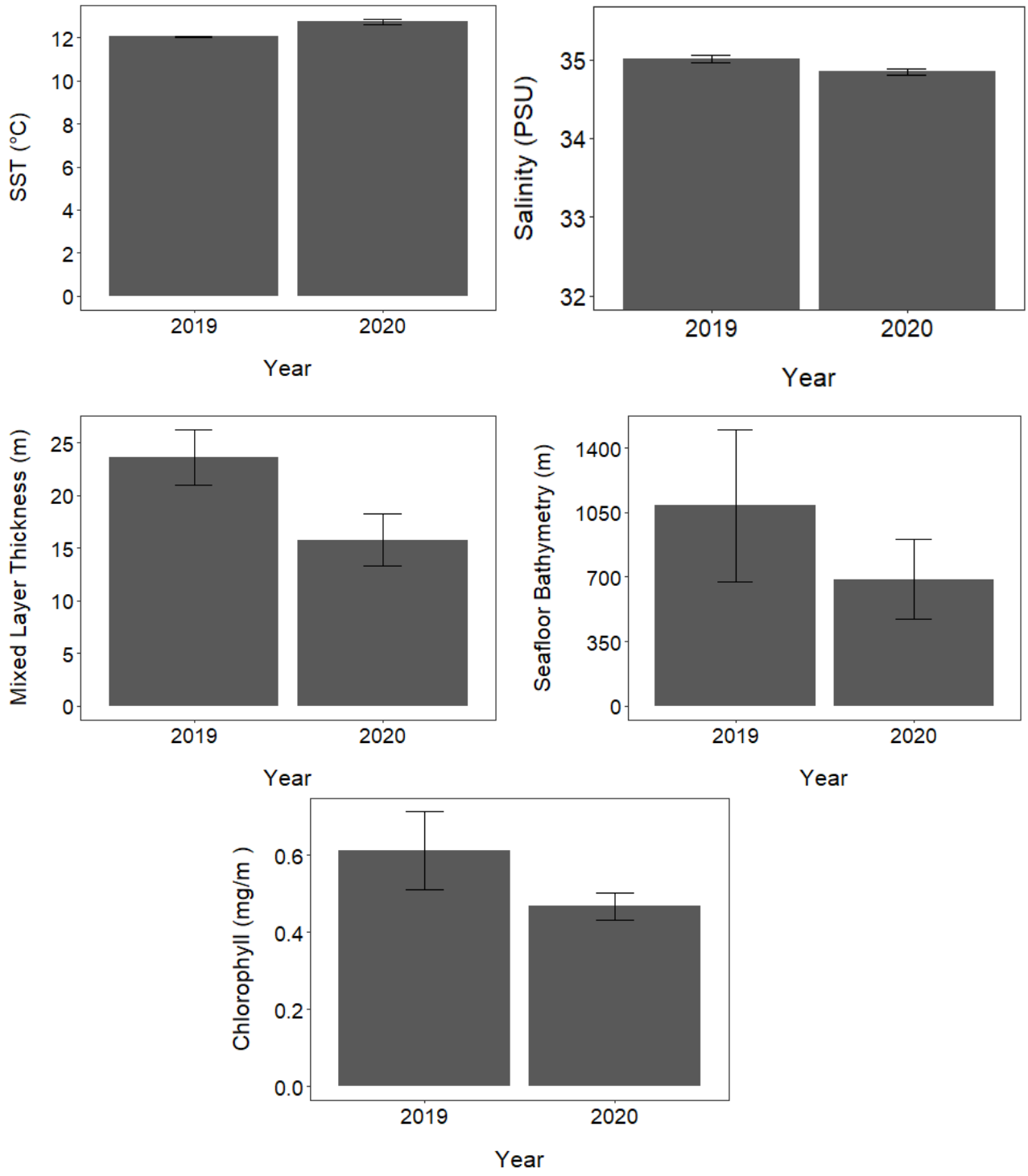

Figure 3.6 The mean (± standard error) of environmental conditions experienced by birds foraging outside Milford Sound fiord, in the ocean between the years of 2019 (n = 6) and 2020 (n =5). Data was collected by aligning the spatial data from foraging birds with the corresponding daily values of oceanographic variables sourced from satellite data.

3.3.5 Impact of environmental factors on the dive behaviour of ocean-foragers

Seafloor bathymetry, chlorophyll-a, SST and salinity were all found to significantly influence the maximum dive depth of ocean-foraging tawaki (Table 3.3). The model including salinity, seafloor bathymetry, chlorophyll-a and SST reportedly explained 55% of the variation in maximum dive depth and 31% of this variation could be attributed to the random effect of bird identity (Table 3.3). Plotted model predictions displayed how the maximum dive depths of tawaki became deeper with higher concentrations of chlorophyll-a, warmer SST and higher salinities (Figure 3.7). Whereas, the dive depths of ocean-foraging tawaki became shallower when foraging over areas of deeper seafloor depths (Figure 3.7).

Seafloor bathymetry, chlorophyll-a and SST significantly influenced the descent velocity of ocean-foraging tawaki (Table 3.3). The model including seafloor bathymetry, chlorophyll-a and SST reportedly explained 53% of the variation in maximum dive depth and 29% of this variation could be attributed to the random effect of bird identity (Table 3.3). Plotted model predictions revealed how the descent velocity of tawaki increased with higher concentrations of chlorophyll-a and higher SST (Figure 3.8). In contrast, descent velocities of ocean-foraging tawaki decreased when foraging over areas of deeper seafloor depths (Figure 3.8).

Seafloor bathymetry had a significant effect on the foraging efficiency of ocean-foraging tawaki (Table 3.3). A model with the fixed factors of seafloor bathymetry explained 11% of the variation in the foraging efficiencies of ocean-foraging tawaki with 4% of this variation being attributable to the random effect of bird identity (Table 3.3). Model predictions showed how the foraging efficiency of ocean-foraging birds increased when foraging over areas with deeper seafloor depths (Figure 3.9).

SST significantly influenced the number of wiggles in the dives of ocean-foraging tawaki (Table 3.3). A model with the fixed factor of SST alone explained 26% of the variation in the number of wiggles per dive of ocean-foraging tawaki with 10% of this variation being attributable to the random effect of bird identity (Table 3.3). Model predictions revealed how the number of wiggles per dive for ocean-foraging tawaki tended to increase with warmer ocean surface temperatures (Figure 3.10).

Table 3. 3 Summary table displaying the model parameters and results for LMMs investigating the effects of environmental variables (chlorophyll-a, seafloor bathymetry, salinity and SST) on three dive parameters (maximum dive depth, descent velocity and foraging efficiency). Dive depth was square root transformed and descent velocity was log10 transformed before being included in the models. A GLMM was used to test the effect of SST on number of wiggles per dive. Bird ID was included as a random effect in the models. P values in bold are below the significance level of <0.05.

Response Variable	Explanatory Variables	Estimate	CI (lwr, upr)		X^2 value	P value	Marginal R^2	Conditional R^2
Max dive depth (m)	Seafloor Bathymetry	-2.80	-3.16	-2.44	232.38	**<0.001**	0.31	0.55
	Chlorophyll	3.17	2.60	3.73	120.90	**<0.001**		
	SST	4.35	3.68	5.01	166.41	**<0.001**		
	Salinity	0.49	0.13	0.85	7.12	**<0.01**		
Descent velocity (ms^{-1})	Seafloor Bathymetry	0.09	0.08	0.11	329.19	**<0.001**	0.29	0.53
	Chlorophyll	-0.14	-0.16	-0.11	142.39	**<0.001**		
	SST	-0.15	-0.18	-0.13	143.47	**<0.001**		
Foraging Efficiency	Seafloor Bathymetry	0.05	0.05	0.07	64.16	**<0.005**	0.04	0.11
Number of Wiggles	SST	0.31	0.19	0.43	25.13	**<0.001**	0.10	0.26

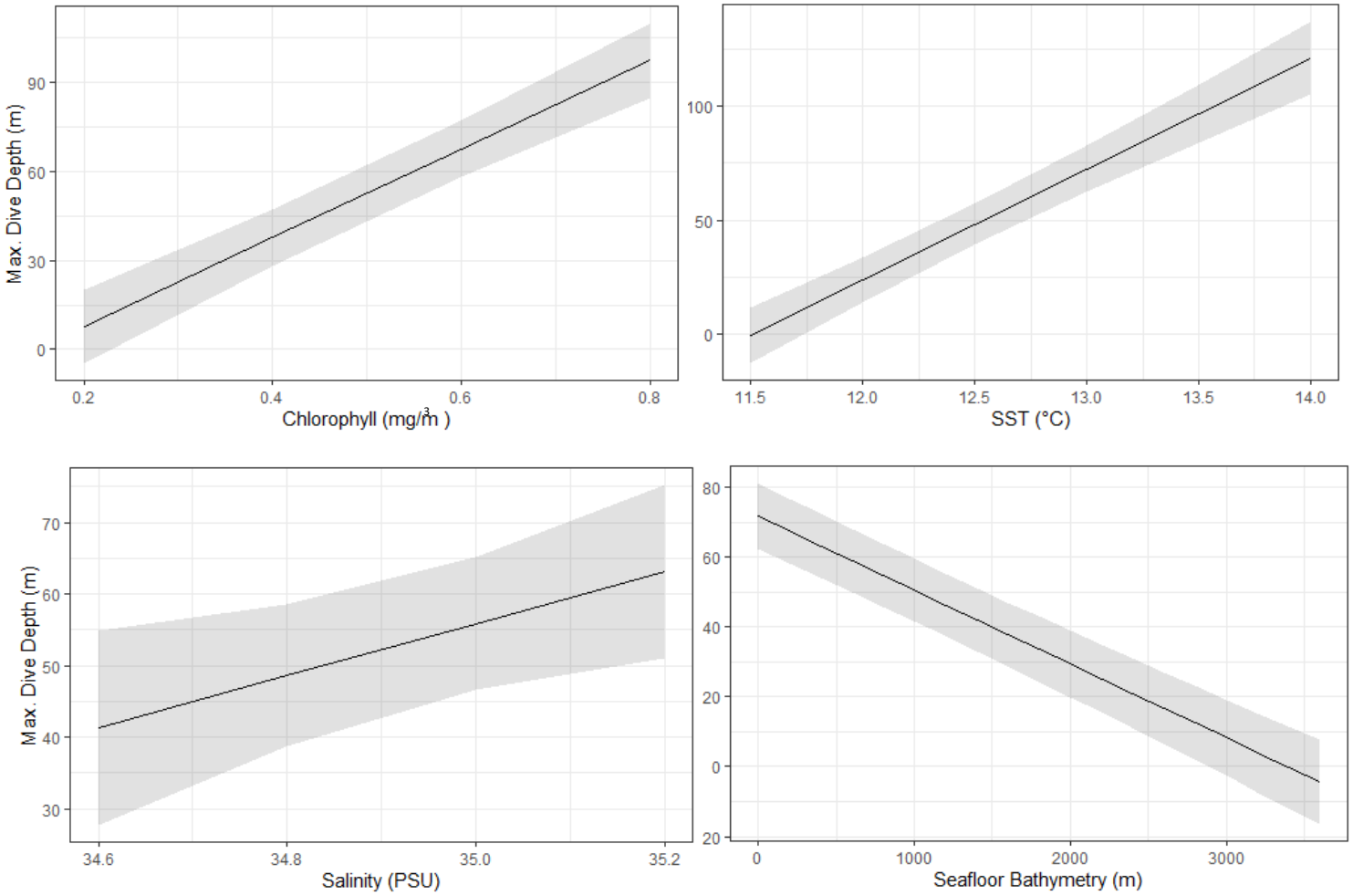

Figure 3.7 Plotted model predictions of the effects of chlorophyll-a, sea surface temperature (SST), salinity and seafloor bathymetry on the maximum dive depth of tawaki foraging in the ocean outside of Milford Sound during guard stage of the 2019 (n = 6) and 2020 (n = 5) breeding seasons.

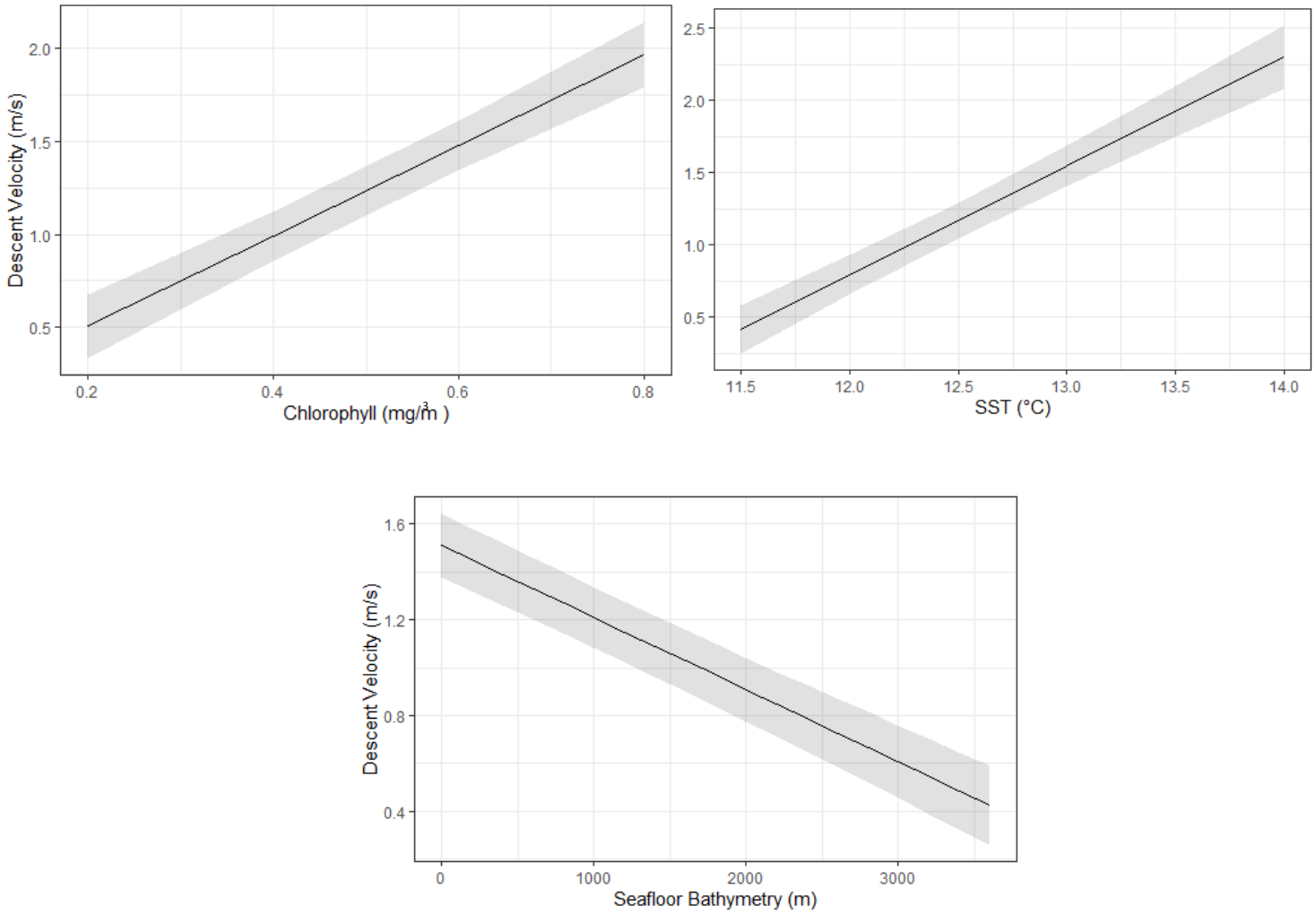

Figure 3.8 Plotted model predictions of the effects of chlorophyll-a, sea surface temperature (SST), and seafloor bathymetry on the descent velocity of tawaki foraging in the ocean outside of Milford Sound during guard stage of the 2019 (n = 6) and 2020 (n = 5) breeding seasons.

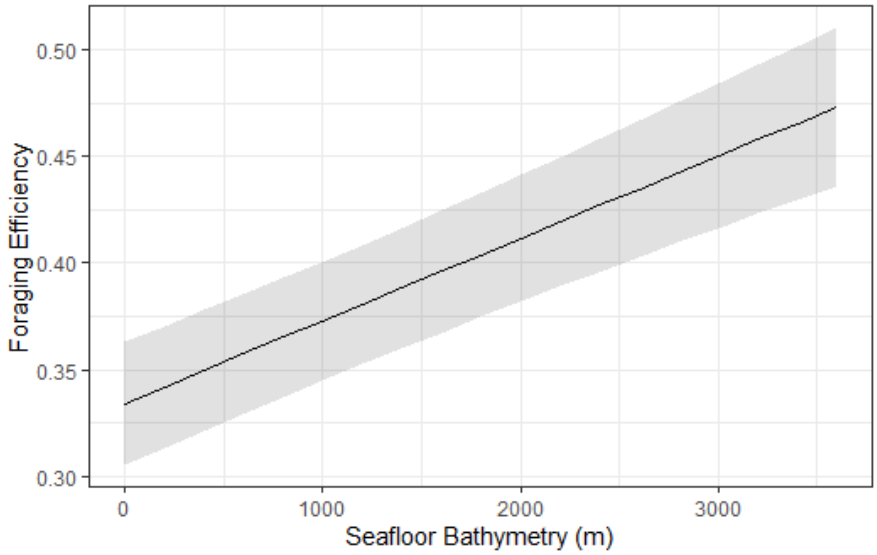

Figure 3.9 Plotted model predictions of the effect of seafloor bathymetry on the foraging efficiency of tawaki foraging in the ocean outside of Milford Sound during guard stage of the 2019 (n = 6) and 2020 (n = 5) breeding seasons.

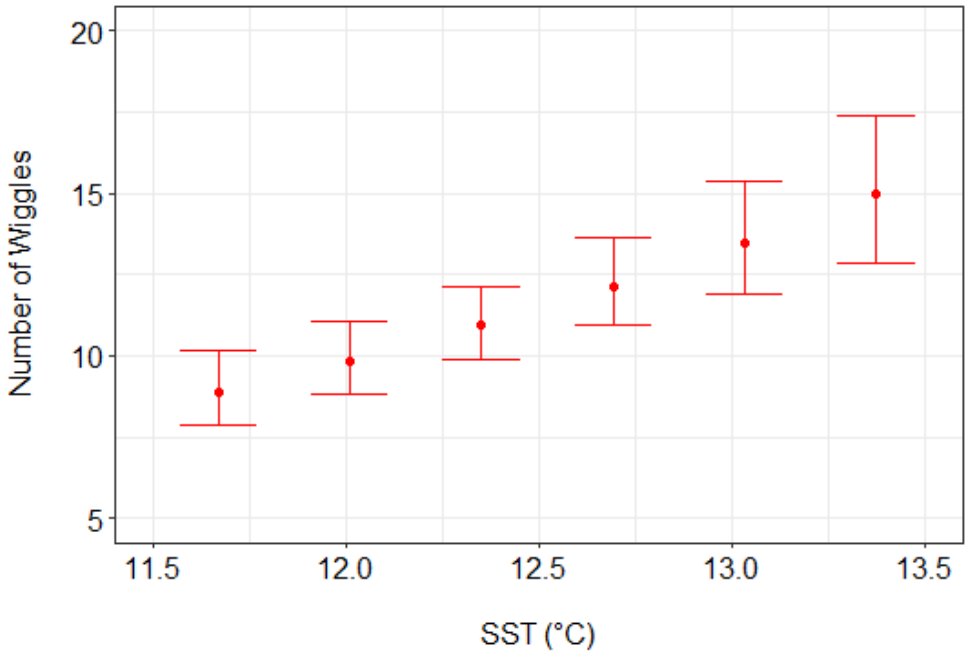

Figure 3.10 Plotted model predictions of the effect of sea surface temperature (SST) on the number of wiggles of tawaki foraging in the ocean outside of Milford Sound during guard stage of the 2019 (n =6) and 2020 (n = 5) breeding seasons.

3.4 Discussion

3.4.1 Do the effects of ENSO explain tawaki foraging behaviour across years?

The El Niño-Southern Oscillation (ENSO) is perhaps one of the most important drivers of inter-annual environmental variability in the waters of the Pacific. There is potential for a correlation between ENSO phases and the foraging conditions within a fiord as research on Scandinavian fiord systems has suggested that processes of exchange between fiords and the adjacent open sea can affect the species composition and abundance of plankton and prey species within a fiord (Lindahl & Perissinotto 1987). Ultimately, the type and strength of the ENSO event occurring in each year did not appear to explain trends in the dive behaviour of Harrison Cove birds throughout 2015-2020. Two years (2016 and 2017) with the exact same ONI of -0.7 (indicating a weak La Niña) revealed contrasting dive behaviours. Furthermore, two years with very similar dive behaviour occurred in 2015 and 2017, with birds completing shallow dives at slower velocities with fewer wiggles per dive. However, conditions in these years were at opposite ends of the spectrum in how they were affected by ENSO, with 2015 being a very strong El Niño year, whereas 2017 was a weak La Niña. It is possible that the unusual foraging behaviour observed in 2019 where Harrison Cove birds exited the fiord and dived much deeper than in previous years could be related to 2019 being the only “normal” year – with conditions closer to neither an El Niño nor La Niña. However, this is unlikely given the context of dive behaviour in the other years showing no clear correlation to the effects of ENSO.

Past research has found that at-sea dive behaviour of penguins and seabirds is affected by the effects of ENSO (Oro et al. 2010; Ancona et al. 2012), namely due to changes in sea surface temperature, and subsequent changes in the abundance of prey (Barber & Chavez 1983). For example, little penguins in Australia exhibited altered dive behaviour such as diving to shallower depths for shorter periods of time during a La Niña event (Berlincourt et al. 2015), suggesting that prey were at higher densities or located more shallowly in the water column during this time (Frederiksen et al. 2006). La Niña events in the New Zealand region are usually associated with warmer sea temperatures on the coastline, and more variable weather patterns (NIWA). For yellow-eyed penguins, these conditions led to change in their dive behaviour towards more pelagic foraging in the weak La Niña events of 2016 and 2017

(Muller et al. 2020). Since guard-stage tawaki from Harrison Cove primarily used the fiord environment for foraging in all past years, apart from 2019, it is likely that their dive behaviour was not significantly affected by the effects of ENSO on the surrounding sea, but instead by the local conditions within the fiord. A similar situation was reported in masked boobies (*Sula dactylatra*) at Clarion Island, whose foraging ecology was unaffected during an El Niño event as their local oceanography did not follow the general ENSO patterns (Lerma et al. 2020).

3.4.2 The fiord-based foraging environment

The local conditions within Milford Sound were notably different between 2019 and 2020, with the fiord having significantly higher rainfall, lower salinity, colder water temperatures, and slightly higher wind speeds in 2020. As tawaki from Harrison Cove foraged mainly in the fiord in 2020 whereas this was not true for 2019, it is possible that the 2020 conditions represent a more favourable fiord foraging environment. The higher rainfall and stronger winds in 2020 would have contributed to the resultant colder temperatures and lower salinity, representing a thicker low salinity layer (LSL) (Gibbs et al. 2000; Gibbs 2001) that was present more consistently in 2020. These conditions have the capacity to create a more favourable foraging environment in the fiord as increased freshwater input can amplify estuarine circulation and increase nutrient input to the fiord, thereby enhancing productivity which can have flow-on effects across the greater food web (Rysgaard et al. 2003).

Significant interactions between salinity, rainfall, and wind speed were found to affect the dive behaviour of fiord-foraging birds. Provided that no recent rainfall has occurred, high salinities in the fiord i.e., a thinner/non-existent LSL, lead tawaki to dive more shallowly and with slower descent velocities. At first, this result seems at odds with our understanding of penguins as visual predators since it is expected that a thinner LSL means there is a reduction in the tannins in the surface layer, resulting in greater light penetration through the water column, thereby allowing tawaki to search visually for deeper prey effectively (Williams 1995). Instead, environmental models indicated that tawaki were diving more shallowly when the LSL was thinner. This may be because a thinner LSL allows marine fish species that are prey for tawaki to rise up in the water column as they are no longer subject to a strong halocline acting as an upper barrier on their distribution (Kaartvedt & Svendsen 1995). Thus,

this enables tawaki to complete shallower dives as their prey is closer to the surface of the water column. With heavy rainfall occurring, however, birds tend to dive deeper and at faster velocities, in more saline fiord waters. The alteration in dive behaviour with rainfall can be attributed to the recent precipitation rapidly building up the freshwater layer again, apparently pushing tawaki to dive deeper past the increasing LSL, to access prey. Since heavy rain events are known to increase turbidity and light attenuation in the upper layers of the fiord, it is also possible that these conditions make it necessary for tawaki to dive deeper past the turbid waters, to locate prey (Meerhoff et al. 2019).

There was a higher degree of uncertainty present in the environmental models predicting the interactive effects of wind speed and rainfall on the dive behaviour of tawaki, and it appeared that only recent heavy rainfall combined with higher wind speeds altered the dive behaviour of tawaki, causing them to dive more shallowly and with slower descent velocities. Wind stress has been recognised in the past as a key mechanism for vertical mixing of the upper water column (Gibbs 2001), with strong winds maximising energetic turbulence and consequently broadening the vertical distributions of some zooplankton (Haury et al. 1990; Goebel et al. 2005). The combined effects of both higher rainfall and wind inputs may be necessary in order for a certain energetic threshold to be met that can noticeably alter the dive patterns of tawaki (Haury et al. 1990). If both strong winds and rain are enhancing mixing in the upper layer of the fiord and expanding the distribution of marine life, tawaki may be able to encounter prey items closer to the surface waters, thus leading them to dive more shallowly and with slower descent velocities. The structure and dynamics of the LSL in New Zealand fiords have been found to respond almost instantaneously to strong wind and rain events, and the environmental models have clearly shown that tawaki respond just as rapidly in modifying their behaviour to match changes in their environment (Gibbs et al. 2000).

Salinity gradients associated with the LSL have been recorded as the principal determinant of biological processes in fiords, including the distribution of organisms (Kregting & Gibbs 2006). It was fitting then, that salinity was the sole significant predictor of the number of wiggles per dive in fiord-foraging tawaki. Although its usefulness has been debated in the past, the number of wiggles per dive can be viewed as an indicator of foraging intensity (Bost et al. 2007; Carroll et al. 2014), with higher numbers of wiggles occurring in dives at lower salinities, suggesting greater foraging activity takes place when the fiord is less saline, and the LSL is thicker. Thus, it appears that what was thought to be a hindrance to the foraging

activity of tawaki – a thicker LSL with greater light attenuation and lessened visibility, may instead provide favourable foraging conditions. The exact mechanism behind this phenomenon is unknown, however, past studies have reported that certain types of zooplankton and fish larvae are restricted to the upper LSL of fiords (Halliday et al. 2001; Piwosz et al. 2009) and it is possible that tawaki are exploiting prey that preferentially inhabit lower salinity waters.

The interface between a thicker LSL with heightened nutrient inputs and the higher salinity water below may also create a unique physical environment that attracts a wider array of prey items for tawaki. In Scandinavian fiords, prey such as sprat can tolerate low salinities and may seek out the more turbid LSL layers to avoid predators (Giske et al. 1994; Landaeta et al. 2011). In a form of ecological irony, the same process may be occurring here and tawaki may actually encounter a higher abundance of sprat in low salinity conditions as the sprat attempt predator avoidance by moving closer to the LSL (Falkenhaug & Dalpadado 2014). Footage from a camera mounted on a tawaki in 2020 has indeed shown that tawaki ingest fish larvae and small sprat-like fish as prey items in Milford Sound (MacLean 2021). It is important to note, however that the environmental model including salinity and rainfall as predictors was estimated to explain about 20% of the variation in the number of wiggles, so there are clearly other factors influencing the foraging activity of tawaki in Milford Sound fiord.

The foraging efficiency of fiord-foraging birds was unaffected by wind speed, rainfall, and even by salinity. This result may seem surprising, but it aligns well with the foraging efficiency of 2020 Harrison Cove birds (see Chapter 2) being remarkably even across the day. Despite changes in the depth to which fiord-foraging birds were diving in response to local environmental conditions, the depths of fiord-foraging tawaki were still principally situated in the upper 20m of the water column. Thus, foraging efficiency should perhaps not be expected to vary greatly when, in comparison to ocean-foraging birds, the majority of dives made by fiord-foraging tawaki are relatively shallow and the birds would not need to rest on the surface for very long post dive.

3.4.3 The oceanic foraging environment

There were notably different conditions present in the marine environment across the years, with the waters that ocean-foraging tawaki exploited in 2020 being on average, warmer and less saline with lower chlorophyll-a concentrations and shallower mixed layer depths. These changes are partly due to the ENSO conditions being “normal” in 2019 while the ENSO phase in September/October of 2020 was of a moderate La Niña (NIWA). The effects of a warm La Niña on the foraging ecology of marine predators appear to be highly variable dependent on the species, colony, and local oceanography (Berlincourt et al. 2015; Dann & Chambers 2013; Lerma et al. 2020).

The model predictions revealed that tawaki dive deeper and with faster descent velocities over areas of warmer SST, higher chlorophyll-a, and shallower bathymetry. This suggests that the prey of tawaki are distributed deeper in the water column in warmer waters, which may be due to pelagic fish species being limited by warmer surface temperatures and thus moving deeper to reach cooler waters below the pycnocline (Sabates et al. 2008). It was unusual that tawaki made deeper dives with faster velocities in areas of high chlorophyll-a as these waters likely have increased light attenuation (Batty et al. 1990; Jaud et al. 2012), which is normally associated with visual predators making shallower dives due to the reduction of light availability limiting their maximum dive depths (Dragon et al. 2010; Jaud et al. 2012). However, it is likely that light availability was not a key limiting factor on the dive depths of ocean-foraging tawaki as visible light is usually able to penetrate the water column up to depths of 150-200m, and no tawaki dived this deep (Akbari et al. 2017). The shallower mixed layer depths observed in 2020, may have also partially offset the decrease in light penetration caused by higher chlorophyll-a concentrations (Kumar et al. 1991; Howard-Williams et al. 1995).

Despite no significant co-linearity detected in the models, there are potentially still some correlations between the environmental factors that are influencing the predictions. For example, SST and chlorophyll-a levels have been reported as positively correlated in areas of shallow bathymetry (Hussein 2021), and since tawaki make deeper dives over shallower seafloor bathymetry, their increased dive depths over areas of higher chlorophyll-a may just be a function of this relationship. Fish may be more likely to aggregate further down the water column in productive areas of shallower coastal bathymetry, leading tawaki to dive deeper to access prey (Miller 2009; Chiaradia et al. 2007). Tawaki in 2020 also spent more of their diving time foraging over shallower neritic waters (56%) than birds from 2019 (37%) that

instead preferred to forage over oceanic waters. This difference in bathymetric foraging preferences across the years may have led to the greater occurrence of deeper dive depths and faster descent velocities shown by ocean-foragers from the Moraine tawaki colony in 2020 (see Chapter 2). In contrast, tawaki that were tracked from Open Bay Island during their breeding season in 2016/2017 were found to spend most of their time in shelf-slope waters (68%) followed by neritic waters (23%) (Poupart et al. 2019). Shelf-slope waters only accounted for 20% of the foraging dives of ocean-foraging tawaki from Milford Sound in 2019 and 2020, indicating that local oceanography plays a significant role in the foraging preferences of tawaki.

Salinity was the weakest predictor of dive behaviour, although the dive depth model suggested the presence of a relationship where tawaki dived deeper in areas of higher salinity. A similar relationship between salinity and foraging behaviour was reported by Poupart et al. (2019) where time spent in an area was influenced by sea-surface salinity, potentially due to lower salinity representing areas of mixing creating favourable foraging conditions (Heath 1985). This aligns with the results of the current study as waters with lower salinity and greater mixing may be more productive and allow tawaki to encounter prey while diving more shallowly. It should also be noted that the random effect of individual identity in the environmental models for dive depth and descent velocity accounted for a substantial amount (30%) of variation in dive behaviour, and this contribution was higher than for the environmental predictors (~25%). Thus, it is evident that in ocean-foraging environments, dive behaviour is just as likely to differ from bird to bird as it is as a result of the oceanic environment.

Seafloor bathymetry was the only variable indicated as a predictor of the foraging efficiency of tawaki. Dives that are made for the purpose of travel/horizontal movement usually have higher foraging efficiencies attached to them than foraging dives (Mattern pers. comm), and taking this into consideration, tawaki might be making more travelling dives in very deep oceanic waters (2000-3000) and passing them by to forage in more favourable conditions instead. This complements the current literature that supports marine predators preferentially foraging in areas of shallower bathymetry (Trathan et al. 2018). It is also possible though, that tawaki are able to forage more efficiently over areas of deeper seafloor bathymetry as they might host more reliable patches of prey or be less depleted by other birds foraging closer inshore (Ashmole 1963; Weimerskirch 1998).

A more direct index of foraging activity, the number of wiggles per dive, was found to increase when tawaki were foraging over areas with warmer surface temperatures. Fluctuations in the abundance and distribution of fish species have been known to occur with changes in water temperature (Barber & Chavez 1983; McInnes et al. 2017). In little penguins, years with warmer water temperatures tend to lead to improved penguin breeding success (Dann & Chambers 2013), and one hypothesis as to why this occurs is due to warmer waters providing greater availability of food (Cullen et al. 2009). There have been instances in some parts of New Zealand where in years of warmer ocean temperatures, there has been enhanced survival of larval and juvenile fish species, as well as the movement of deeper water species to coastal waters (Basher 1998). A greater abundance of prey and/or the presence of a different suite of prey items in warmer waters may be linked to the higher amount of foraging activity, represented by the greater number of wiggles per dive shown by ocean-foraging tawaki. Since tawaki were also diving at deeper depths at warmer temperatures, they may have been foraging for particular prey species that require a more complex pursuit than shallower water species, resulting in a higher number of undulations while diving.

3.4.4 Conclusions

This study is the first to present how fine-scale environmental variables might be influencing the dive behaviour of tawaki foraging in different environments. The combined effects of salinity and rainfall had particularly clear effects on the dive depths and descent velocities of tawaki, while salinity was the strongest predictor of foraging activity in terms of the number of wiggles per dive. Tawaki actively modify their dive behaviour according to the changing environment of the fiord, and birds made deeper dives and experienced greater foraging activity when the LSL was thicker. Although one would think that the foraging of visual predators would be negatively impacted by thicker LSLs creating a darker environment, the LSL is, after all, one of the unique environmental attributes of fiord systems, and if its presence was really a hindrance to the foraging behaviour of tawaki, they would likely exit the fiord to forage in the ocean. Tawaki that did forage in the ocean outside of Milford Sound primarily dived deeper and experienced enhanced foraging activity over warmer waters, particularly those that occurred in 2020 during the moderate La Niña and may have increased the abundance of prey and caused distributional shifts of fish in the water column.

Environmental data gathered for ocean-foraging tawaki were limited by the degree of spatial resolution that could be obtained for each variable, with SST, salinity and bathymetry having the most spatially detailed datasets (see Appendix 3, Table A3.1). Furthermore, only daily values could be sourced for oceanic monitoring data. In contrast, data sourced for fiord-foraging tawaki were limited spatially by the position of the mooring buoy within the fiord but could be matched to dive data on a temporally fine scale (hourly). Although the mooring buoy in the fiord gives insight to variation in temperature and salinity across Milford Sound, future studies on the impact of the environment variables may benefit from having multiple buoys situated both in the middle of the fiord, at either side of the fiord walls and at the entrance. This would be valuable to further pinpoint the environmental foraging preferences of tawaki and investigate their dive behaviour on both a spatial and temporal fine scale as studies have shown that sub-surface salinity and LSL thickness varies as a function of distance to the fiord entrance and freshwater inputs (i.e. glacier fed waterfalls) (Gibbs et al. 2000).

Chapter 4: General Discussion

4.1 Summary of key findings

For the future protection and conservation of a relatively understudied penguin such as tawaki, it is vital to establish a foundation of knowledge on their foraging ecology, especially for those colonies that breed in the unique system of a fiord. As an environment, fiords are relevant to a significant proportion of the tawaki population, with Fiordland being one of the three key regions they inhabit. The inter-annual and inter-colony foraging dynamics of tawaki from Milford Sound, New Zealand were examined, along with the environmental influences that may be affecting the dive behaviour of tawaki foraging in different environments - the open ocean or the fiord.

Tawaki from the outer-fiord colony of Moraine were found to forage exclusively in the open sea, swimming further from their colony site and completing longer trips over greater distances than their counterparts from the inner-fiord colony of Harrison Cove. Birds from Harrison Cove foraged both within the fiord and out in the coastal ocean in 2019 but primarily foraged within the fiord in 2020. This led to differences in the dive behaviour of Harrison Cove tawaki across the years as birds made deeper and longer dives with faster descent velocities in 2019 than in 2020, when their foraging was much more efficient and their dives were notably shallower, mainly occurring within the upper 30m of the water column. The dive behaviour of Moraine birds also altered across the two years with 2019 being a year of shorter, shallower dives with slower dive velocities compared to the deeper dives that took place more often at depths of 70-120 metres. The foraging ranges of Moraine birds were also smaller, and they went on shorter trips, covering shorter distances in 2020 compared to 2019.

Changes in the oceanic environment across 2019 and 2020 may be the reason behind differences in the foraging behaviour of tawaki, especially since the breeding season of 2020 occurred in a La Niña year with warmer waters and lower coastal chlorophyll-a. Environmental models revealed that ocean-foraging tawaki engaged in higher foraging activity and made deeper dives with faster descent velocities over warmer water; their dive behaviour was also affected by salinity, concentrations of chlorophyll-a and seafloor

bathymetry. Tawaki that foraged within the fiord were found to have their dive behaviour impacted solely by local conditions in the fiord, such as the interactive effects of salinity, rainfall and wind speed, as these factors contribute to the thickness and degree of mixing in the low salinity layer (LSL). In particular, a thicker LSL, as indicated by low salinity in the upper fiord waters, appears to increase foraging activity and cause tawaki to dive deeper, revealing that a thicker LSL may in fact, create more foraging opportunities for tawaki and does not necessarily compromise foraging due to the birds being visually impaired by the lower light environment.

It is also clear that tawaki have a high degree of behavioural flexibility, both in the plasticity exhibited in dive behaviours on a trip-to-trip basis as well as in their ability to modify their behaviour based on the environmental conditions they are exposed to.

4.2 The variability of the oceanic foraging environment

As central-place foragers during the breeding season, tawaki are required to adapt their foraging behaviour in response to environmental variation, and this was evident through the changes in their foraging behaviour across 2019 and 2020. In particular, birds from the Moraine colony adopted alternative foraging strategies in 2019 and 2020. In 2019, birds from Moraine expended more energy going on longer trips over greater distances, but they also dived more shallowly. In contrast, 2020 Moraine birds saved energy by making generally shorter trips closer to their colony site and foraging primarily in neritic waters but exhibited greater foraging effort in their dive behaviour by making deeper dives more consistently. Based on these results, it is hard to determine whether one year was a “better” foraging year than the other. Studies on other penguins usually suggest that years where individuals are able to forage more shallowly represent more favourable foraging conditions, suggesting 2019 was the better year (Ponganis et al. 2000; Berlincourt et al. 2015). However, taking the foraging trip parameters into account, there appeared to be more feeding opportunities closer to the colony in 2020, suggesting that this year was more favourable (Burke & Montevecchi 2009; Robertson et al. 2014; Ramos et al. 2018). Either way, adapting to altered conditions in the oceanic environment by adjusting aspects of either their foraging trips or dive behaviour, allowed tawaki to maximise their energy efficiency and successfully raise offspring, as was

observed in both years. Adjustments of trip length and dive behaviour between seasons due to changes in foraging conditions have also been observed in other seabird species (Garthe et al. 2011; Sommerfield et al. 2015).

Due to the prevalence of La Niña conditions in 2020, the waters around the coastal ocean outside of Milford Sound were significantly warmer than in 2019, and the environmental models suggested that the dive depths and foraging activity of ocean-foraging tawaki increased as a result. The literature is inconclusive as to whether warmer water temperatures improve (Pinaudn & Weimerskirch 2002; Cullen et al. 2009) or hinder (Guinet et al. 1998; Weimerskirch et al. 2001; Ramos et al. 2018) the foraging success of seabirds. Off the Bonney Coast of Australia, where La Niña exerts the opposite influence, little penguins have experienced favourable foraging conditions in the past due to cooler waters increasing local productivity and prey availability (Berlincourt et al. 2015). Therefore, it was initially thought that the warmer SST and lower chlorophyll-a concentrations in New Zealand waters during the warm La Niña of 2020 may have resulted in a less productive feeding environment for tawaki foraging in the ocean (Aruga & Monsi 1963). There seemed to be support for this hypothesis since these conditions corresponded with the deeper dives exhibited by the ocean-foraging tawaki from the Moraine colony in 2020, that were indicative of higher foraging effort. Despite this, the foraging efficiencies of Moraine birds were still higher in 2020 than in 2019 and the abundance of prey appeared to have shifted closer to the colony. Furthermore, other colonies of penguins have had more successful foraging years during breeding seasons when water temperatures were warmer (Cullen et al. 2009), so clearly there is a high degree of local variability.

The higher levels of chlorophyll-a in areas that ocean-foraging tawaki were exploiting in 2020 might also not be the best indicator of a productive foraging environment. While some researchers have found sub-surface chlorophyll-a to be important in affecting the foraging decisions of marine predators (Scott et al. 2010; Nowak et al. 2020), others have found significant spatial mismatches between high levels of chlorophyll-a and the true abundance and distribution of prey (Grémillet et al. 2008). Vincent et al. (1991) stated that remote-sensed chlorophyll-a concentrations were an inaccurate index of the water column chlorophyll-a stock in coastal waters of the South Island as they were influenced by coastal run-off. This emphasises the importance of assessing multiple environmental variables that may have

contributed to the productivity and foraging success of seabirds, to obtain a fuller picture of the physical factors affecting them.

This study has shown how tawaki from the Moraine colony alternated foraging strategies dependent on the marine conditions in 2019 when the ENSO was in a “normal” phase and in 2020 when the ENSO was in a La Niña phase. Both years allowed sufficient foraging to take place, as evidenced by observations of two chicks being raised in some nests, well past the stage where one should have died (St Clair 1992). It would be interesting to see how Moraine birds cope with the marine conditions present in an El Niño year (colder sea surface temperatures, stronger south westerly winds, higher rainfall), particularly since tawaki foraging from other coastal sites further up the South Island failed to adequately forage for their chicks in the most recent severe El Niño of 2015 (Mattern & Ellenberg 2015). Birds from the Moraine colony, while never foraging solely within the fiord in 2019 or 2020, do technically have the option to switch from ocean-foraging to fiord-foraging if oceanic feeding conditions were deplorable. Although Harrison Cove birds have shown flexibility as to whether they forage within or outside the fiord, it remains unknown as to whether Moraine birds possess the same level of behavioural flexibility. If they do, this will bode well for the future survival and breeding success of the colony in times of food scarcity in the coastal marine environment.

4.3 The fiord as a unique foraging refuge

Most Harrison Cove birds were able to forage completely within Milford Sound fiord in 2020, travelling an average maximum distance of only 8km from their colony site, which was a three-fold reduction in the maximum foraging radii of the Moraine birds from their colony. Not only did fiord-foraging Harrison Cove birds complete shorter trips, but they also dived more shallowly than birds foraging in the open ocean. Both their dive behaviour and their shorter foraging trips make for a more energy-efficient strategy than that exhibited by ocean-foraging birds, and it is unclear as to why birds from all colonies breeding within the fiord do no take advantage of the fiord environment for foraging. Birds from Moraine may be closer to the ocean, but their colony is technically still situated within the fiord limits, and if they were to travel to the innermost part of the fiord, this would still only be a total distance of 11km

away from their colony, compared to the 24km they travel on average to find profitable foraging grounds in the ocean.

It is unknown what makes New Zealand fiords such a productive foraging environment for marine predators, especially since most studies on the ecology of the upper trophic levels of fiord systems have been conducted in Scandinavian arctic fiords or Chilean fiords. In these systems it has been shown through biodiversity surveys that a plethora of novel species exist, and other organisms show distributions across habitats that are at odds with their preferences elsewhere (Försterra & Häussermann 2003; Esteves et al. 2007; Sinniger & Häussermann 2009). Fiords provide a substantial degree of habitat complexity to marine life, and many fish species are known to seek out areas that are structurally complex (Chittaro 2004).

In Alaska, schools of forage fish make seasonal movements into the inner fiords and increase prey availability for seabird chicks (Day et al. 1999; Arimitsu et al. 2012). Glacial fiords have also been shown to provide key spawning habitat and nursery zones for small pelagic fish that are important prey species for marine predators (Arimitsu et al. 2008). Similar mechanisms may be occurring in the fiords of New Zealand, increasing prey availability for the New Zealand fur seals (*Arctocephalus forster*) and penguins that inhabit them. The walls of New Zealand fiords also reportedly represent areas of high productivity as they are regularly enriched by the accumulation of detritus and rockfall (Grange 1991; Matthews and Heimdal 1979; McLeod and Wing 2007). In a recent study, the distribution of bottlenose dolphins (*Tursiops truncatus*) in Doubtful Sound was found to be positively associated with distance to the fiord walls, likely due to the walls providing greater opportunity for feeding on reef fish (Bennington 2021).

Environmental models revealed that the presence of a stronger LSL, as indicated by the salinity of the sub-surface fiord waters, led to greater foraging activity and deeper dives. This trend somewhat debunks the idea that a thick LSL leads to compromised foraging due to the birds being visually impaired by the lower light environment. Some past studies have found that the lower light environment in a fiord may actually be beneficial for the foraging of marine predators as although phytoplankton may be limited, macrozooplankton are often abundant closer to the surface waters, possibly due to them missing the presence of photic cues for diel migration (Arimitsu et al. 2012). Readily available zooplankton higher up in the

water column due to a thicker LSL could mean greater prey availability for tawaki and explain why Harrison Cove birds may benefit from foraging within the fiord when the LSL is thicker and recent rainfall has taken place. Heavy rainfall and higher wind speeds combined, also increased the dive depths of fiord-foraging birds. Waters with high turbidity, caused by strong rainfall and wind may further aid in improving the availability of prey fish due to the absence of visual cues that allow fish to gather in dense schools and avoid predators (Partridge and Pitcher 1980). There was significantly less daily rainfall in 2019, and this would have led to clearer waters, a thinner LSL and consequently, a lowered abundance of easily accessible prey in the fiord, which may have been part of the reason why more Harrison Cove tawaki exited the fiord to forage.

Although we can speculate as to why more Harrison Cove tawaki foraged in the ocean in 2019, more research is required to understand the environmental controls on the spatial foraging decisions of tawaki. What is clear, however, is that the fiord generally acts as a 'buffer' against the influence of the ocean, with submerged sills isolating the cool and stratified inner-fiord habitats from the coastal waters outside (Mayr et al. 2011). The role of Milford Sound as a refuge was first postulated when researchers saw how the Harrison Cove birds successfully foraged exclusively in the fiord during the El Niño event of 2015 while other ocean-foraging coastal tawaki colonies suffered (Mattern & Ellenberg 2015). This has been further supported by the current study in 2019 as birds from Harrison Cove exerted considerably less energy foraging within the fiord than those from Moraine foraging out in the ocean. More detailed data needs to be gathered on how differences in energy expenditure might result in reproductive consequences, although it was observed in 2015 that Harrison Cove birds were able to raise two chicks while making short foraging trips within the fiord, while the longer coastal foraging trips of Jackson Head birds led to chick starvation and reproductive failure (Mattern & Ellenberg 2015)

The phenomenon of refugial habitats during El Niño has also been documented in the Canal de Ballenas in the Central Gulf of California where highly mobile marine animals, including whales, dolphins and boobies, left areas of reduced productivity and flocked to the Canal during the 1983 El Niño as productivity here was high irrespective of the ENSO phase (Tershy et al. 1991). Aid et al. (1985) also reported that the Gulf of Panama may have been an example of a high productivity refuge during the 1983 El Niño as sea surface temperatures there remained relatively cool and were accompanied by high abundances of seabirds. Milford

Sound clearly has the potential to act in the same way, serving as a refuge to marine life during unfavourable foraging years and protecting tawaki from adverse conditions in the oceanic environment.

4.4 Implications for conservation

The extent to which Milford Sound and the other fiords of New Zealand act as refugia for tawaki is currently unknown. Tawaki from inner-fiord colonies such as Harrison Cove evidently know how to use the fiord as a profitable foraging habitat, but it is yet unknown whether tawaki from outer-fiord colonies such as Moraine are able to make the most of the fiord during years of lowered oceanic productivity and harsh foraging conditions. It is important, either way, that the fiord systems of New Zealand are protected due to their unique environmental value and their ability to provide sufficient foraging opportunities for tawaki with minimum energy expenditure. Thus, the protection of fiord systems may be able to further the conservation of tawaki in the face of climatic uncertainty. Currently, this protection is being fulfilled in the form of the Piopiotahi–Milford Sound Marine Reserve which covers 690 ha across the northern side of Milford Sound. Fiord-foraging tawaki in 2019 and 2020 foraged on both sides of the fiord, however, there was often a substantial amount of activity around Stirling Falls on the northern side – likely due to this feature being a rich source of freshwater input as well as being within the marine reserve.

Disregarding theories of inter-colony segregation, one reason why Moraine birds do not preferentially forage in the fiord while Harrison Cove birds do, could be their locations relative to the marine reserve. On the northern side, as soon as Harrison Cove bird leave their colony to forage, they are exposed to the rich environment of the inner fiord that has been protected from harvest. On the southern side, Moraine birds exit their colony into an environment that has a more substantial oceanic influence due to its proximity to the fiord entrance. Furthermore, Moraine birds are not instantly met with an environment that has been protected from anthropogenic harvesting activities, and thus there may appear to be poorer food availability within the fiord, causing them to turn to foraging in the open ocean. Milford Sound is one of the most popular amateur fishing areas in Fiordland and although the greatest recreational takes occur around coastal Milford, there is still a considerable amount of fishing activity in the inner fiord in the unprotected zones (Davey & Hartill 2011).

Marine reserves play a vital role in maintaining balance in the age structure of marine organisms by providing refuges from human activity that allow fish or invertebrates to safely spawn (Berkeley et al. 2004, Birkeland & Dayton 2005). Although the rest of Milford Sound is likely gaining spill over benefits from the Milford Marine Reserve, it still seems somewhat counter-intuitive to protect only half of the fiord system when many of its higher trophic level inhabitants are mobile. Especially if the lack of protection on one side is causing some tawaki to forgo the abundant feeding opportunities the fiord may provide. Ideal management of Milford Sound would call for the preservation of the entire ecosystem, to safeguard the integrity of the complex food webs and ensure the ecosystem is functioning at its full potential (Chapin et al. 2000).

The protection of fiords as refugia for tawaki is particularly important considering that adverse marine conditions and the frequency of El Niño events are expected to increase (Cai et al. 2014; Cai et al. 2015). Although seabirds can be adept at altering their foraging behaviour to buffer environmental changes in prey distributions (Litzow et al. 2002; Garthe et al. 2011), there eco-physiological limits to foraging plasticity (Somerfield et al. 2015). If prey availability drops below a key threshold during an environmental disturbance, tawaki from Moraine could find open-ocean foraging unprofitable and this could lead to the same negative consequences on reproduction and survival reported in tawaki from the Jackson Head colony (Mattern & Ellenberg 2015) and other seabirds (Harding et al. 2007; Grémillet et al. 2009). Changes to the environmental conditions of the ocean outside Milford Sound in 2019 and 2020 were clearly within the eco-physiological limits of Moraine tawaki. However, considering shifts to the availability of prey are expected to intensify in the foreseeable future due to climate change (Grémillet et al. 2009), the Moraine colony, and other coastal populations of tawaki should be monitored to uncover the extent of their foraging plasticity and behavioural limitations.

Notwithstanding the future impacts of climate change, the results of my study have shown that tawaki do possess a high degree of behavioural flexibility, and we can be hopeful for their future. Through investigating changes in stable isotope values during the pre-moult period associated with an El Niño event, White (2020) also found that tawaki appeared to adapt to different prey sources while at sea. In 2020, tawaki were even downgraded from a vulnerable IUCN ranking to the ‘near threatened’ category, and they are indeed faring better than some

other New Zealand penguin species such as the yellow-eyed penguin (Mattern et al. 2017). With continued research and monitoring work under The Tawaki Project, the outlook for the conservation of tawaki, especially in fiord systems, is optimistic.

4.5 The 2020 Season and COVID-19

An unforeseen factor during the 2020 breeding season was that due to COVID-19, the tourism and boat activity in Milford Sound was much lower than normal. Under usual circumstances, Milford Sound is one of New Zealand's most popular tourist destinations with visitor numbers reaching almost 1 million in 2018 (MacDonald 2021). Boat cruises through the fiord are the main tourist activity and tawaki are often a key attraction on these tours. Although the detrimental effects of tourism have been described in detail for the dolphins of Fiordland (Lusseau et al. 2006; Guerra et al. 2014), the effects of boat traffic on tawaki are unknown. However, along with the potential of risk of propeller strikes to diving penguins (as reported in other species e.g., Cannell et al. 2016), the cumulative underwater noise from fleets of operating tourist boats may also impact the foraging of tawaki and their prey species (Mattern & Wilson 2018).

What is notable, is that in 2020, when tourism and boat traffic was significantly reduced, fiord-foraging tawaki from Harrison Cove had the highest foraging efficiencies reported to occur in any year from 2015-2020. An exact correlation cannot be deduced from this, but it is possible that the absence of high intensity boat activity influenced the foraging behaviour of 2020 Harrison Cove birds, potentially acting as a confounder in the current study. Apart from the slightly higher foraging efficiencies though, 2020 Harrison Cove birds generally behaved the same as in previous years (2015-2018). More research is required to understand the relative risk to tawaki from boating operations in Milford Sound, although it seems that for now, COVID-19 has aided in scaling back the level of tourism intensity.

4.6 Future research

The Tawaki Project began in 2014 and has included monitoring and tracking of the Harrison Cove colony over their breeding seasons since 2015. There lies significant merit in developing long term datasets such as these, and the current study has displayed the additional importance of monitoring multiple colonies within the same fiord. Continued monitoring will allow researchers to follow changes in habitat use, foraging behaviour, and reproduction through time, to further develop an understanding of how to best manage tawaki in these unique fiord ecosystems.

In 2020, footage from a camera-borne Harrison Cove tawaki was successfully obtained, revealing for the first time some of the types of prey items that tawaki are foraging on within the fiord (MacLean 2021). The next step is to replicate these camera deployments in future seasons to glean further information on the preferred prey of tawaki. Further insights could be gained by gathering footage of the foraging trips of Moraine birds, to determine exactly how different the prey pool is in the ocean outside Milford Sound to that within the fiord. White (2020) highlighted how stable isotope analyses comparing Harrison Cove birds to Southern Island and coastal-based tawaki colonies did not reveal any significant differences in trophic niches. However, it may be that differences exist on a finer scale and can only be quantified in detail by identifying certain species that are part of the bird's diets.

DNA sampling of the faeces from different colonies is currently ongoing and may provide further insights into changes in tawaki foraging ecology. The methods of camera-logging and DNA sampling will also be of value in determining how substantially the diets of ocean-foraging tawaki from the Moraine colony change between years. For example, the diets of white-chinned petrels (*Procellaria aequinoctialis*) shifted as a result of the bathymetry i.e., foraging over nearby shelf waters or deeper oceanic waters (Catard et al. 2000). As ocean-foragers from the Moraine colony used oceanic waters more often in 2019 but preferred neritic waters in 2020, it is quite possible that they were foraging on different prey. Since there is an absence of concrete information on tawaki prey species composition, further investigations are vital to solidify the interpretation of the current results.

This study has established that divergent foraging strategies exist between inner and outer fiord tawaki colonies, and future research should work towards identifying whether this is a common phenomenon through replication at the fiord level. Fiordland has a total of 14 fiords across which replication could be achieved, provided there are enough tawaki colonies. This

process is already underway in Doubtful Sound, with other fiords such as Dusky Sound and Breaksea also having reportedly healthy numbers of tawaki to work with, if sites are accessible (Russ et al.1992). It is unknown whether there are fitness-level consequences for fiord-breeding tawaki foraging in different environments, and the pursuit of more information on fledgling rates and chick growth rates across colonies may shine light on this question, although it is hard to quantify reproductive success once tawaki chicks are mobile and creching. Collecting more information on the foraging movements of Milford Sound tawaki during the post-guard and/or incubation stages would also be useful, especially to determine the degree to which inner-fiord birds might expand their range and forage outside the fiord since foraging ranges usually increase during these stages (Poupart et al. 2019).

Finally, given the title of penguins as ‘marine sentinels’, fiord-breeding tawaki may be able to fit into the role of ‘fiord sentinels’ and be used as an indicator of the health of fiord ecosystems. Already, fiord systems across the world are preparing for the impact of climate change (Iriarte et al. 2010; Marín et al. 2013; Bianchi et al. 2020). These ecosystems are expected to change considerably over the next few decades regarding freshwater inputs, stratification and temperature which will likely lead to flow-on effects on fiord food webs. In New Zealand we are only just scratching the surface of exploring our fiord-based ecosystems and don’t necessarily have thorough baseline data on each system. Therefore, tawaki present the perfect opportunity to align the monitoring of the species with uncovering a more comprehensive understanding of ecosystem function within fiords. This will improve our ability to detect changes in fiord food webs and respond to potential threats to these systems, ensuring that their preservation is prioritised.

4.7 Conclusions

The initial goals of this research were to investigate differences in the foraging behaviour between an inner-fiord and an outer-fiord colony of tawaki over two years and to determine which environmental factors were driving their dive behaviour. It was thought that tawaki from a colony at the fiord entrance would show greater flexibility in foraging as they have immediate access to both the oceanic and fiord environments. However, birds from this outer-fiord colony of Moraine never once fully accessed the fiord environment and instead it was

tawaki from the inner-fiord colony of Harrison Cove that made occasional foraging trips outside of the fiord (more so in 2019 than 2020) while primarily using the fiord in 2020. Birds from Moraine were shown to alter their foraging ranges and dive behaviour as a result of altered oceanographic conditions in 2019 and 2020, however, research is still needed to address whether they are able to use the fiord to evade poor oceanic conditions during future environmental disturbances. This research demonstrates the importance of studying the behaviour and spatial use of multiple nearby colonies, as even those within a 9km radius of each other may exhibit very different foraging strategies which could impact their future survival.

This research has expanded our knowledge of the environmental factors that are influencing the foraging behaviour of guard-stage tawaki. Coarse environmental data on the phase and strength of ENSO events was found to be unhelpful as a tool to assess trends in the dive behaviour of tawaki from an inner-fiord colony. Instead, environmental models with fine-scale temporal resolution at hourly intervals revealed that the interactive effects of recent rainfall, wind speed and salinity at 0.5m depth were all important in predicting the dive behaviour of fiord-foraging tawaki. Salinity, as an indicator of the thickness of the LSL appeared to be the most important predictor in determining the birds' dive behaviour and foraging activity, revealing that the presence of an LSL is beneficial rather than detrimental to fiord-foragers.

For ocean-foragers, a whole different set of oceanographic conditions, modelled with spatial remote-sensing data, were used to examine the role of salinity, seafloor bathymetry, SST and chlorophyll-a levels on the dive behaviour of tawaki. These methods enabled me to uncover meaningful associations between tawaki and environmental conditions over a local scale, at a time when birds are restricted to central-place foraging. Often the focus in the literature is on the impact of environmental processes over macro or meso scales when birds are out on pre- or post-moult foraging trips (Hull et al. 1997; Mattern et al. 2018). However, when birds are at the most critical period of their life stage i.e., breeding to ensure the future viability of their population, it is often local-scale conditions that are most important. Tawaki, especially those from outer-fiord colonies, should continue to be monitored over their breeding season in the future, in order to create a long-term dataset with which to evaluate their true flexibility across a range of environmental fluctuations.

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Appendices

Appendix 1

Tawaki body mass and correlation with dive parameters

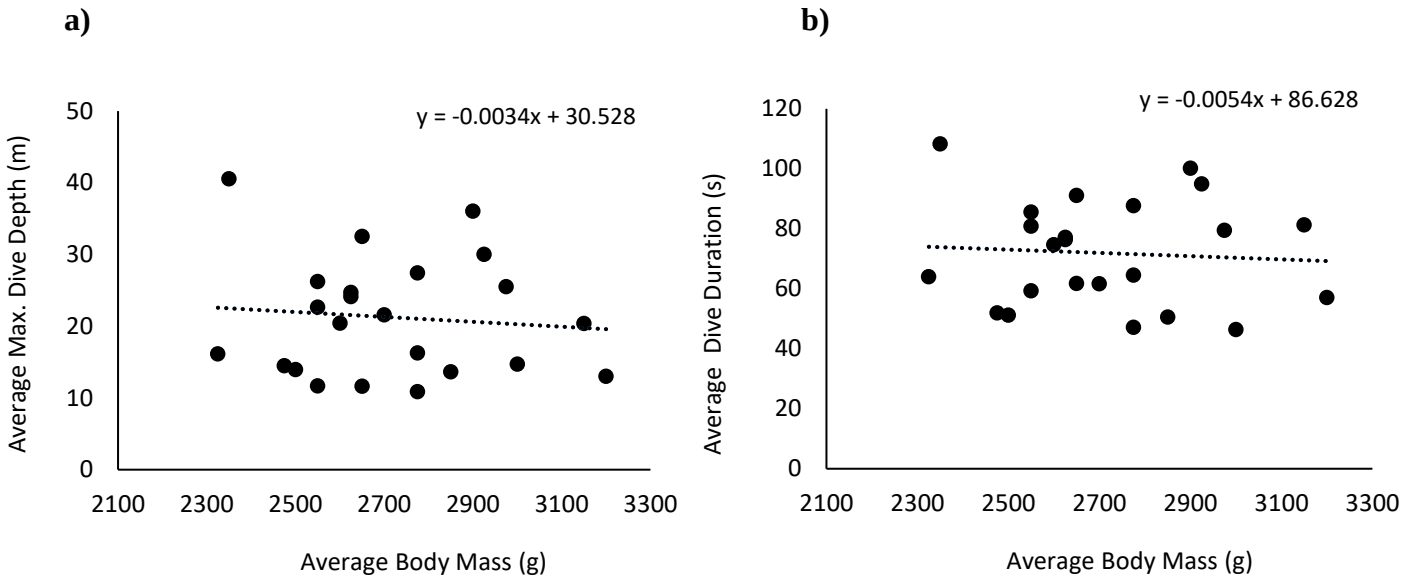

Figure A1.1 Graphs displaying the lack of a correlative relationship between average body mass of tawaki and their average **a)** dive depth and **b)** dive duration. n = 22.

Table A1.1 Table displaying the average body mass of each individual tawaki that were weighed once prior to device deployment and once after device removal. Averages per colony per year are also

	2019		**2020**	
	Moraine	Harrison Cove	Moraine	Harrison Cove
Body Mass (g)	2500	2975	2625	2650
	3000	2475	2900	3150
	2600	2550	2700	3200
	2625	2650	2350	2325
	2850		2775	2775
	2550			2925
				2550
				2775
Average	**2687.5**	**2662.5**	**2670**	**2793.75**

Appendix 2

Additional material on tawaki dive behaviour

Table A2.1 Full summary table displaying the means, standard deviations and model parameters of all dive parameters for tawaki from the Moraine (MO) and Harrison Cove colony sites in Milford Sound during the guard stage of the breeding season in years 2019 and 2020. Means were calculated using the average of individual means. Trip ID nested within Bird ID were including as random effects in each model which were fit as either a Linear Mixed Model (LMM) or a Generalized Linear Mixed Model (GLMM) for which the appropriate error structure was chosen. P values in bold are under the set significance level of <0.05, df = 1.

	2019		2020		Model Outputs						
Response Variable	Moraine	Harrison Cove	Moraine	Harrison Cove	Explanatory Variables	Model	Estimate	CI (lwr, upr)		S.E.	X^2 value	P value
Dive activity (dives h^{-1})	40.9 ± 29.2	34.8 ± 20.6	30.5 ± 18.3	37.7 ± 18.3	Site (MO)	GLMM - Negative Binomial	0.05	-0.22	0.32	0.14	1.68	0.20
					Year (2020)		0.12	-0.16	0.40	0.14	0.39	0.53
					Site (MO):Year (2020)		-0.32	-0.69	0.05	0.19	2.82	0.09
Number of wiggles per dive	7.6 ± 5.8	8.3 ± 5.9	9.1 ± 6.6	8.7 ± 5.6	Site (MO)	GLMM - Negative Binomial	-0.06	-0.31	0.19	0.13	0.02	0.90
					Year (2020)		0.10	-0.13	0.33	0.12	2.87	0.09
					Site (MO):Year (2020)		0.08	-0.24	0.40	0.16	0.23	0.63
Dive duration (s)	63.4 ± 38.6	77.0 ± 42.3	87.0 ± 48.5	74.2 ± 37.7	Site (MO)	LMM	-11.08	-32.50	10.35	10.93	1.28	0.26
					Year (2020)		-8.99	10.96	8.82	10.18	1.11	0.29
					Site (MO):Year (2020)		32.35	4.41	60.30	14.26	5.15	**<0.05**
Max dive depth (m)	18.2 ± 17.0	24.7 ± 20.6	30.1 ± 28.1	16.3 ± 11.8	Site (MO)	GLMM - Gamma	-0.22	-0.64	-0.60	0.16	6.67	**<0.01**
					Year (2020)		-0.38	-0.77	-0.73	-0.04	0.19	0.66
					Site (MO):Year (2020)		0.84	0.46	0.36	1.32	11.93	**<0.001**
Descent rate (ms^{-1})	0.85 ± 0.38	0.94 ± 0.38	1.05 ± 0.43	0.86 ± 0.32	Site (MO)	LMM	-0.08	-0.20	0.05	0.06	5.63	**0.018**
					Year (2020)		-0.08	-0.19	0.03	0.06	2.33	0.13
					Site (MO):Year (2020)		0.26	0.11	0.42	0.08	11.03	**<0.001**
Ascent rate (ms^{-1})	0.83 ± 0.34	0.86 ± 0.35	0.92 ± 0.36	0.87 ± 0.37	Site (MO)	LMM	-0.03	-0.12	0.06	0.05	0.87	0.35
					Year (2020)		-0.02	-0.10	0.06	0.04	0.96	0.33
					Site (MO):Year (2020)		0.08	-0.03	0.19	0.06	2.13	0.14
Bottom time (s)	30.3 ± 31.9	35.1 ± 21.0	40.0 ± 23.0	36.9 ± 20.7	Site (MO)	GLMM - Gamma	-0.12	-0.37	0.14	0.13	0.10	0.75
					Year (2020)		0.02	-0.21	0.26	0.12	3.01	0.08
					Site (MO):Year (2020)		0.24	-0.08	0.57	0.17	2.12	0.15
Time at surface (s)	14.0 ± 25.2	14.2 ± 16.3	16.8 ± 22.2	14.9 ± 23.5	Site (MO)	GLMM - Gamma	0.01	-0.26	0.28	0.14	2.26	0.13
					Year (2020)		-0.03	-0.28	0.22	0.13	0.67	0.41
					Site (MO):Year (2020)		0.20	-0.14	0.54	0.18	1.29	0.26
Diving efficiency	0.82 ± 0.15	0.84 ± 0.11	0.84 ± 0.12	0.84 ± 0.12	Site (MO)	GLMM - Gamma	-0.02	-0.07	0.03	0.02	0.13	0.72
					Year (2020)		0.00	-0.04	0.04	0.02	0.53	0.47
					Site (MO):Year (2020)		0.02	-0.03	0.08	0.03	0.66	0.42
Foraging Efficiency	0.37 ± 0.17	0.38 ± 0.15	0.40 ± 0.17	0.42 ± 0.17	Site (MO)	GLMM - Gamma	-0.03	-0.12	0.06	0.05	3.57	0.06
					Year (2020)		0.13	0.05	0.21	0.04	12.13	**<0.001**
					Site (MO):Year (2020)		-0.05	-0.17	0.07	0.06	0.72	0.40

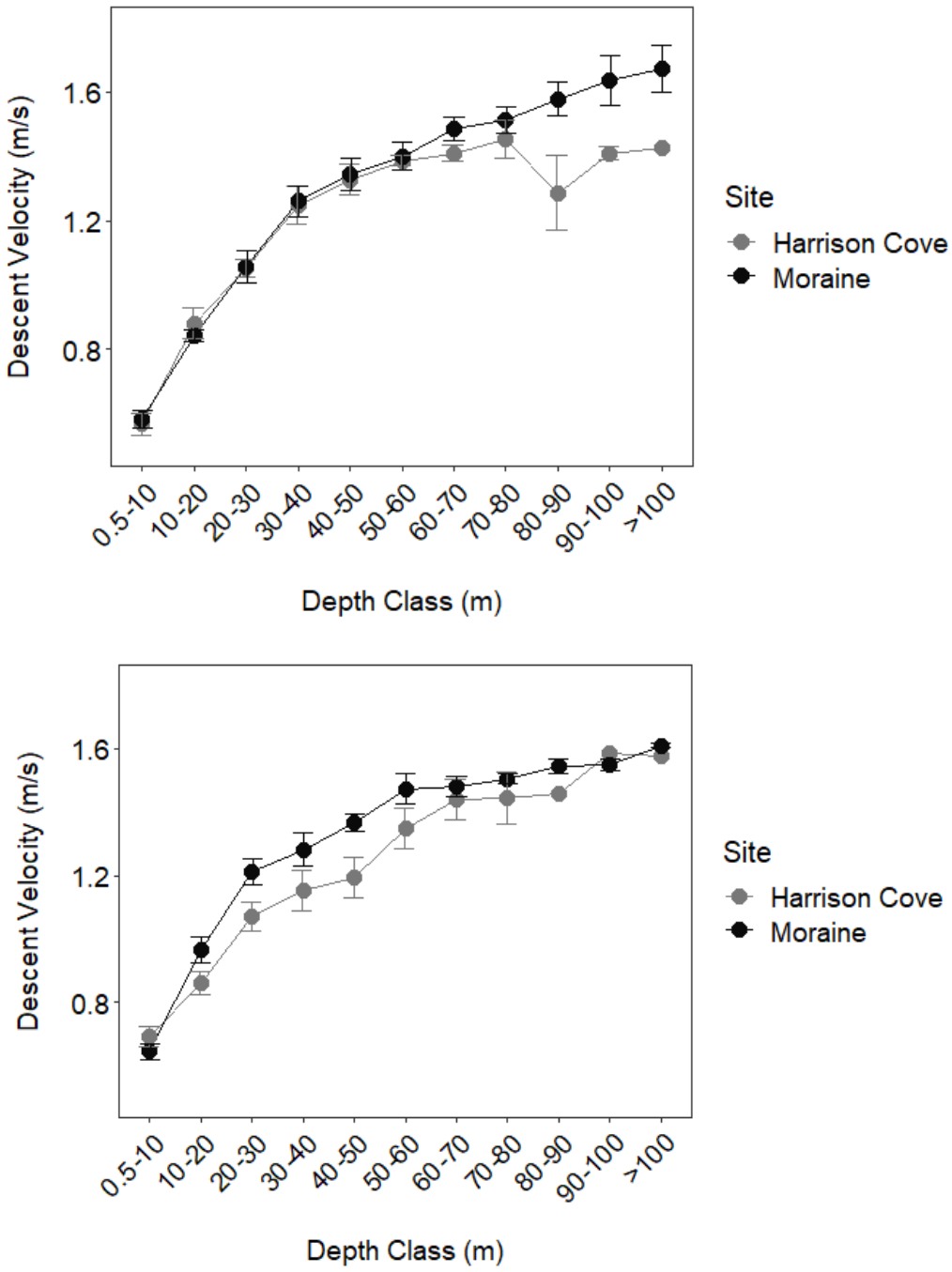

Figure A2.1 Comparison of mean descent rate in metres per second (±standard error) at depth classes of 10m intervals for tawaki from two colonies in Milford Sound (Moraine and Harrison Cove), during the guard stage of the 2019 (top) and 2020 (bottom) breeding seasons. Harrison Cove: n = 4 (2019), n = 8 (2020); Moraine: n = 6 (2019), n = 5 (2020).

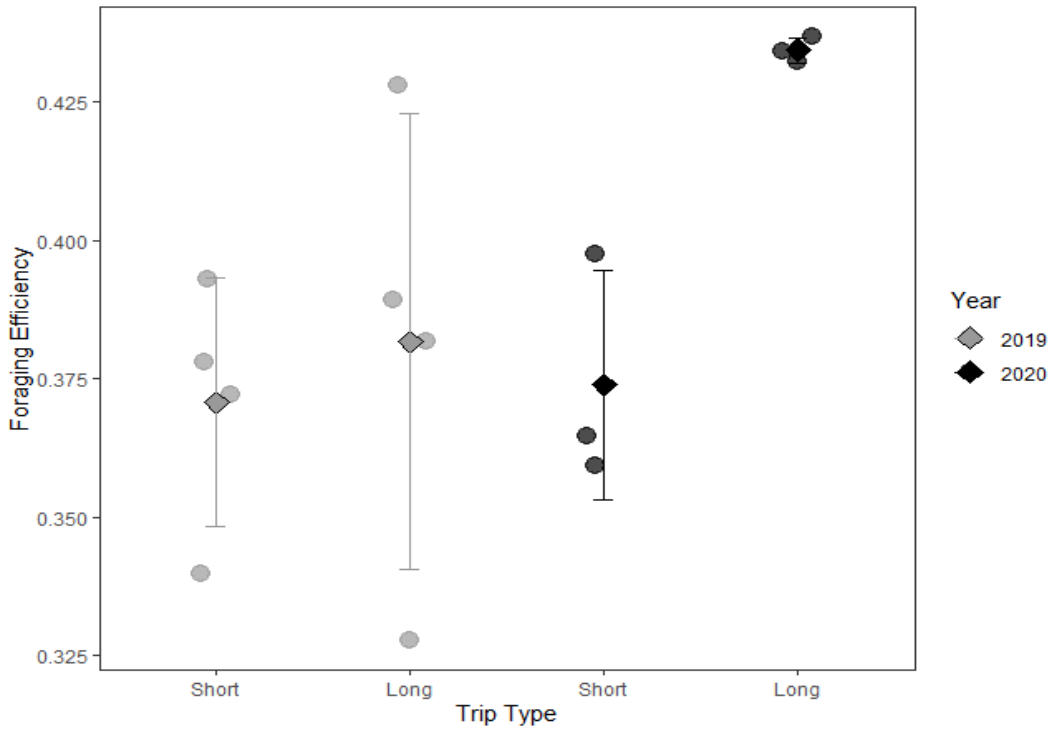

Figure A2.2 Comparison of individual means for the foraging efficiencies of long (>24 hours) and short (<24 hours) trips from tawaki of the Moraine colony in Milford Sound, during the guard stage of the 2019 and 2020 breeding seasons. 2019: n = 6; 2020: n = 5. Diamonds represent the overall mean for that year and trip type.

Appendix 3

Additional material on environmental models

Table A3.1 Environmental data used to model the dive behaviour of ocean-foraging and fiord-foraging tawaki. Seafloor bathymetry was downloaded from https://www.niwa.co.nz/our-science/oceans/bathymetry, mixed layer thickness, salinity, and chlorophyll-a concentration from https://coastwatch.pfeg.noaa.gov/, and sea surface temperature from http://marine.copernicus.eu/. Salinity and temperature of fiord waters from an oceanographic mooring at Milford Marina were provided by Meridian Energy, wind speed and rainfall was taken from an electronic weather station in Milford Sound and downloaded from https://cliflo.niwa.co.nz. True spatial resolution for fiord variables could be between 0m and 13km since the data from a stationary mooring and weather station in Milford Marina was aligned to the dive behaviour of birds that may have been located anywhere throughout the length of the 13km fiord.

Environmental variable (unit)	Spatial / temporal resolution / sensor depth (-) or height (+)	Source
Ocean Variables		
Seafloor bathymetry (m)	250m / - / -	New Zealand Regional Bathymetry 2016
Sea surface temperature (°C)	0.01° / daily / -0.5m	Multi-scale Ultra-high Resolution (MUR) SST Analysis fv04.1
Mixed layer thickness (m)	0.08° / daily / -	Global_analysis_forecast_PHY_001_024
Sub surface salinity (PSU)	0.08° / daily /- 0.5m	Global_analysis_forecast_PHY_001_024
Chlorophyll-a concentration (mg/m^3)	0.25° / daily / -0.5m	Global_analysis_forecast_BIO_001_028
Fiord Variables		
Salinity (PSU)	- / hourly / -0.5m	Meridian energy dataset
Temperature (°C)	- / hourly / -0.5m	Meridian energy dataset
Wind speed (km/h)	- / hourly / 3m	NIWA weather station
Rainfall (mm)	- / hourly / 3m	NIWA weather station

Table A3.2 Initial testing for the inclusion of variables in the final environmental models for the dive behaviour (maximum dive depth, descent velocity, foraging efficiency and number of wiggles) of ocean-foraging tawaki using two measures – the relative importance of variables after AIC (Akaike Information Criteria) model selection and the model averaged co-efficients and confidence intervals. Relative importance measures in bold indicate values >0.95.
95% confidence intervals (CI) in bold indicate intervals that do not include zero.

			AIC Model Averaging	
Response Variable	Explanatory Variables	Relative Importance	Coefficient	CI (lwr, upr)
Max. Dive Depth	Chl	**1.00**	3.17	**2.60, 3.74**
	Bathy	**1.00**	-2.76	**-3.15, -2.36**
	SST	**1.00**	4.33	**3.64, 5.02**
	Sal	0.88	0.48	**0.04, 0.92**
	Year (2020)	0.43	0.01	-0.30, 0.18
	MLT	0.27	-0.06	-1.03, 1.05
Descent Velocity	Chl	**1.00**	-0.14	**-0.16, -0.11**
	Bathy	**1.00**	0.09	**0.07, 0.10**
	SST	**1.00**	-0.15	**-0.17, -0.12**
	Sal	0.04	-0.00	-0.01, 0.00
	Year (2020)	0.03	-0.00	-0.01, 0.01
	MLT	<0.01	-0.00	-0.00, 0.00
Foraging Efficiency	Bathy	**0.99**	0.05	**0.03, 0.08**
	Chl	0.65	-0.04	-0.10, 0.02
	Year (2020)	0.31	-0.02	-0.09, 0.05
	Salinity	0.23	0.00	-0.02, 0.03
	SST	0.10	-0.00	-0.03, 0.02
	MLT	0.01		
Number of Wiggles	SST	**1.00**	0.28	**0.15,0.40**
	MLT	0.75	0.05	-0.02, 0.12
	Sal	0.48	0.02	-0.44, 0.09
	Chl	0.31	-0.01	-0.09, 0.06
	Bathy	0.31	0.00	-0.04, 0.04